SPATIAL AND TEMPORAL ECOLOGY OF A COLONIAL WATERBIRD: THE DISTRIBUTION AND ABUNDANCE OF NESTING COMMON EIDERS (*Somateria mollissima*) IN LABRADOR

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Spatial and Temporal Ecology of a Colonial Waterbird: The Distribution and Abundance of Nesting Common Eiders (*Somateria mollissima*) in Labrador

by

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ABSTRACT: Understanding patterns of animal distribution and abundance and their causes is at the heart of ecological investigations with implications for conservation, resource management, theoretical development and testing. Surveys to evaluate the localized distribution and abundance of common eiders (*Somateria mollissima*) nesting in Labrador were conducted from 1998 to 2003. Information was compiled and analysed with respect to clutch size, nest initiation, nest density, abundance, population trend, spatial distribution, colony dynamics, as well as interspecific and abiotic habitat relationships. Eiders showed a north south-clinal variation in nest initiation with birds in the south laying earlier then birds in the north. There was significant interaction between annual and regional variation in life history parameters (nest initiation, clutch size, egg volume) and regional differences in nest abundance and nest density, with the lowest densities in Hopedale, while Nain and Rigolet were comparably high. Overall, eider populations were increasing. Colony dynamics and local population turnover were investigated, and colonization rate was greater than extinction rate, but these varied by region. Interspecific relationships were investigated and significant positive associations were found between nesting eiders and nesting Larids (*Larus argentatus* and *L. marinus*), and gulls seemed to track eider colonies over time, but eiders did not track gull colonies. No evidence of a significant relationship between nesting eiders and intertidal resources were found. Negative relationships were documented between nesting eiders, landscape features and ice. This was attributed to increased access to breeding islands by terrestrial predators; however other factors such as colder conditions, or reduced access to prey because of ice obstruction or ice scour might be at play. The effect of spring ice on nesting eiders in Labrador has profound implications for understanding the biological

consequences of long-term global climate change. This thesis represents some of the first published information on eider ecology in Labrador, a focal species with ecological and cultural importance, and this research has implications for the regional, national, international conservation and management of common eiders. Findings were interpreted in the context metapopulation theory, source sink population dynamics, conspecific attraction, and the ideal free distribution.

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I am indebted to many people for their help with this project. In particular I would like to thank my wife (Donna) and daughter (Natasha) for enduring my long hours and obsessive-compulsive drive to finish this dissertation. I thank my parents (Bernard and Rose) for providing me the opportunity, as a child, to experience a traditional Labrador lifestyle, this experience more than any other that drew me to wildlife biology and allowed me to balance my love of science with my love of nature. I also thank Bernard and George Chaulk for teaching me how to hunt, fish and trap, and for teaching me about my heritage and how closely we Labradorians are linked to the plants, mammals, fish and birds that occupy this big land. I also owe a great debt of gratitude to Judy Rowell, throughout my professional career she has been my benefactor, and her efforts opened many doors allowing me to pursue both an M.Sc and PhD.

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FOREWORD

In 1998, on behalf of the Canadian Wildlife Service (CWS) with the support of Bruce Turner, Pierre Ryan, and numerous people in Labrador, initiated a program to document common eider (*Somateria mollissima*) population trends. The general methods were simple: I recorded nest counts on islands in various archipelagos on the Labrador coast, and repeated these surveys over a number of years, adding new islands and archipelagos as time progressed. In anticipation of other uses of the data, and prior to the start of the study, I decided to track a number of variables, including clutch size, nest status, nest age, nest habitat, island habitat, island location, nests of other species, and presence of nest bowls. These variables were subsequently expanded to include egg size, and intertidal habitat measurements.

Early in the program it was clear that eiders had previously used some islands for nesting that were currently vacant. In 1999, I added two new archipelagos to the study and by the end of the second field season it became apparent that eiders were unevenly distributed within and across archipelagos, and that many apparently suitable islands were

empty, while apparently marginal islands were occupied. I began to think about possible explanations for these patterns, and a vague shadow of a dissertation began to emerge.

In the summer of 2002 I had the opportunity to work with Dr. Greg Robertson. Based on our discussions I became convinced that the data I had accumulated could be used as the basis for a PhD dissertation. In 2003 Dr. Bill Montevecchi offered me a position as a PhD candidate, and subsequently I enrolled as a full time student in the Cognitive and Behavioural Ecology PhD program at Memorial University of Newfoundland. Both Bill and Greg agreed to be on my supervisory committee. My dissertation proposal gradually developed as I considered a series of competing hypothesis to explain various distribution and abundance patterns that I had observed in the field. These included the Ideal Free Distribution (Fretwell and Lucas 1970), Conspecific Attraction (Stamps 1988), Metapopulation Theory (Levin 1969, Hanski 1999), and Source Sink Population Dynamics (Pulliam 1988). The following dissertation is the product of field research combined with theoretically driven hypotheses.

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GENERAL INTRODUCTION

Background

In the 21st century, climate change, habitat loss, over-harvesting and pollution threaten biodiversity and ecosystem functioning (Cox and Moore 2000, Krebs 2001). The imminent threat of global ecosystem change has pushed the conservation paradigm to the forefront of ecology (Primack 1998, Rushton et al. 2004). Conservation managers require information on the habitat requirements, population dynamics, spatial distribution of organisms and community interactions in order to make effective conservation decisions. In turn, this information can be used to assess population status and/or influence land use and harvest policy. It is through these public management processes that otherwise esoteric research can have practical implications.

Unfortunately, not all species are equally studied, and often those species that receive the most research attention are not always those which are most threatened. Nevertheless, well studied organisms, populations and/or ecosystems can often provide insight into general ecological processes upon which scientists and managers can extrapolate general principles that can be widely applied in the conservation struggle.

In this chapter I introduce the general conservation paradigm which underlies most current ecological research. I also identify my research questions, briefly summarize the contents of the subsequent chapters and provide the linkages that tie the chapters together into an integrated thesis. I use a manuscript format and specific theoretical contexts are presented in each chapter. In the final chapter I synthesize, discuss and summarize my findings.

Research Questions

The research questions which underlie this thesis are: 1) What factors influence the spatial distribution of avian nesting populations? and 2) what are the ecological patterns that arise as consequences of spatial behavioral processes? Specifically, I am interested in why common eiders (*Somateria mollissima*) nest where they nest? I investigate intrinsic and extrinsic factors that influence the distribution and abundance of common eiders.

The intrinsic mechanisms that I investigate that may influence population dynamics are nest initiation, clutch size, colony dynamics, distribution, abundance and coloniality. I also investigate how distribution and abundance may interact. In fact, according to some researchers (Hanski 1999, Gaston 2003) some of the most interesting theoretical questions in current ecology address intra-specific distribution and abundance relationships.

In order to understand the relationship between intra-specific distribution and abundance, it is important to express spatial distributions numerically as a function of incidence and/or occupancy rate, which in turn allows for quantitative analysis. For example, if abundance in a given area is zero, then the distribution (i.e., incidence) in that area is also zero. However, the relationship between incidence and abundance can be positive, negative or neutral and a growing body of ecological literature explores this relationship (Hanski 1982, Bock and Ricklefs 1983, Brown 1984, Wright 1991, Gaston and Blackburn 1996, Johnson 1998, Venier and Fahrig 1998).

Generally, abundant organisms are widely dispersed while rare species have smaller geographic ranges (Gaston and Blackburn 1996, Johnson 1998), with few

exceptions. For example, the common grackle (*Quiscalus quiscula*) is declining in abundance but increasing in distribution (Gaston and Curnutt 1998). Yet, most species that have been investigated have exhibited positive intra-specific incidence and abundance relationships (Hanski 1982, 1999, Nee et al. 1991, Gaston and Curnutt 1998).

The relationship between distribution and abundance has implications for understanding small and large-scale population change. In fact, insight into distribution and abundance interactions can have major implications for resource management and public policy decisions. For example, Krebs (2001) outlined how scientists and managers failed with respect to the management of the northern cod (*Gadus morhua)* fishery. In short, these groups did not fully consider the relationship between distribution and abundance when assessing population status. We now know that as the cod population declined, the fish aggregated, and in turn, the fishermen also aggregated, keeping catch rates high (Krebs 2001). Seeing no change in catch rates, scientist and managers did not adjust quotas, combined with the increased effort and technological improvements in gear that made it possible to catch more fish before the northern cod population collapsed due to over-fishing (Harris 1990, Krebs 2001). This example demonstrates how failing to understand relationships between abundance and distribution can have serious ramifications for conservation and natural resource management.

The incident and abundance relationship also has important links to self organizing systems theory. Self organizing systems may shed light on emergent properties of ecological systems (Perry 1995, Joergensen et al. 1998, Roces 2002). One of the main characteristics of self organizing systems is the requirement for positive (or negative) feedback loops, such as those that are often associated with intra-specific

incidence and abundance curves. The implication of positive relationships between incidence and abundance is that animals influence their own distributions through 1) rescue effect (Brown and Kodric Brown 1977), behavioural mechanisms such as those described by the ideal free distribution (Fretwell and Lucas 1970), source sink population dynamics (Pulliam 1988), and/or metapopulation processes (Hanski 1999). Furthermore, recognizing properties inherent to self organizing systems could aid in discerning interrelationships between these theoretical frameworks.

Metapopulation theory was first proposed by Levins (1969) as a mathematical model to explain patterns of local extinction and colonization in pests. It considers spatial and temporal change in distribution and abundance. Metapopulation characteristics include habitat patchiness, local population extinction, colonization from adjacent local populations, and population connectivity without complete mixing (Hanski 1991). Metapopulation concepts have been widely applied across taxa (Gulve 1994, Hanski and Thomas 1994, Akcakaya and Atwood 1997, Appelt and Poethke 1997, Barbraud et al. 2003).

One area of conservation ecology where metapopulation theory is having a major impact is habitat protection. At one time, heated debate existed over the SLOSS ("single large or several small" reserves) debate about the effectiveness of protected area design (Primack 1998). The debate is ongoing. On the one hand, there are strong arguments for the design of large reserves (Primack 1998). In fact, one of the main findings of island biogeography is that larger islands support more species (MacArthur and Wilson 1967).

However, there are growing examples in the literature from many taxa that demonstrate the utility of a metapopulation concepts and functioning. Thus for species

that have a patchy distribution, protecting many small, connected patch networks that support multiple local populations may be desirable. According to metapopulation theory, higher numbers of connected local populations can translate into greater resistance to overall extinction (Hanski 1999), which is the primary goal of conservation ecology (Primack 1998). This resistance to extinction is achieved through resistance to inbreeding and re-colonization of empty patches (Simberloff and Cox 1987). For those species that function as metapopulations, high connectivity among local populations could have negative impacts by facilitating disease transmission, forest fires, predators, etc. (Krebs 2001). The caveat here is that not all species function as metapopulations and for these species, fragmented reserves may have negative consequences for both distribution and abundance (Primack 1998, Burel and Baudry 2003).

Much attention has also been paid to the artificial fragmentation of landscapes, though less attention has been directed at the role of natural fragmentation in ecosystem functioning. Labrador is a relatively pristine environment compared to many regions in North America. Industrial activity is currently at low levels but mining, hydroelectricity, forestry and oil developments are either ongoing or inevitable. Thus, rates of artificial fragmentation are expected to rise quickly in the near future. Understanding spatial population dynamics in expansive and naturally patchy ecosystems could aid managers and scientists in mitigating the negative effects of industrial activities.

Finally, intrinsic and extrinsic factors often interact to influence distribution and abundance. Extrinsic factors may include: predation, disease, food availability, inter-specific competition, mutualism, commensalisms, weather and climate. The simultaneous modeling of intrinsic and extrinsic interactions is complex, and impractical;

most times it is simpler and more practical to model simple relationships and extrapolate their influence to overall population processes. Throughout this thesis, I have taken a simple approach to modeling spatial and temporal interactions with respect to distribution and abundance.

The Study Subject

This thesis explores basic questions in behavioural, population and spatial ecology using the common eider as the study subject. The common eider is a well studied colonial sea duck that nests on marine islands. Throughout their range, the spatial population dynamics of common eiders have not been well studied, and in terms of a regional context in Labrador even their basic biology and ecology is not well known. For example, basic reproductive parameters and population trend have never been described. This thesis attempts to answer some general theoretical questions with respect to eider distribution and abundance, but it begins by addressing some basic reproductive and ecological gaps specific to the Labrador sub-arctic region of the eiders' range.

With seven sub-species worldwide, common eiders are an example of microevolution at work. Within their global range, Labrador is particularly interesting for studies of spatial population structure because two eider sub-species co-occur and nest there (Mendall 1980, Chaffey 2004). In addition, like many northern species, eiders are influenced by ice conditions (Goudie et al. 2000) and may be useful as an indicator species with which we can gauge the biological effects of climate and oceanographic change.

Nesting eiders are also easy to monitor and their gregarious behaviour makes them an ideal species to study spatial dispersion and population dynamics. The colonial

behaviour of eiders also makes them prone to disease transmission at greater rates than solitary organisms (Wittenberger and Hunt 1985, Kwan 2004). Disease transmission is an important topic given escalating concerns about West Nile virus, avian cholera, and avian influenza in wild bird populations. Understanding processes that influence population connectivity could be very important for understanding patterns of disease transmission at local, regional and global scales. While not the focus of this thesis, it is possible that some of the findings presented in this thesis could be extrapolated to avian epidemiology. With this general background, I studied common eiders to investigate population dynamics, spatial ecology, colonial behaviour, interspecific relationships and landscape ecology in a northern marine ecosystem.

Chapter Linkages

These first three chapters contain substantial information on natural history that will be of significance to researchers, managers, and individuals interested in eider ecology and conservation. The last two chapters have broader theoretical implications that relate to population dynamics and behavioral processes in eiders, migratory birds, colonial species, and spatially structured populations in general. In Chapter 2, I discuss some basic concepts such as eider clutch size, nest initiation, nest density, nest status, and island occupancy. This chapter, published in *Arctic* (Chaulk et al. 2005a), assesses the reproductive characteristics at the archipelago and sub-species scale. The findings of this chapter support previously documented geographic zonation with respect to eider sub-species affiliation. These findings also aid in understanding population affiliation and as such may also provide valuable information with respect to population grouping and harvest management.

My findings also help us understand broad scale population structure and spatial distribution patterns. In fact, I use these findings as theoretical background in later chapters when I suggest that metapopulation theory is an applicable theoretical framework to study common eiders. For example, the existence of sub-speciation in common eiders at large geographic scales implies limited mixing across the species' range (Wright 1940), which in turn is consistent with metapopulation assumptions (Hanski 1991).

Chapter 3, published in *Polar Research* (Chaulk et al. 2004), is also a natural history paper that focuses on similar reproductive characteristics to those presented in Chapter 2. However, Chapter 3 includes data from different archipelagos, different years, employs different statistical techniques, includes additional analyses, and the general question of the chapter is different from Chapter 2. Chapter 3 investigates how regional and annual interactions vary with respect to their magnitude and direction when the effects of space and time are modeled together.

Specifically, I asked whether annual patterns of variation were maintained across regions, or whether traits varied independently within regions across the years. The findings in Chapter 3 support the conclusions presented in Chapter 2 with respect to geographic zonation and sub-species affiliation, but in addition they shed new light on spatial and temporal interactions. I found that both year and region are important and that under most circumstances they interact. In addition I found that significant variation can occur at smaller spatial scales, such as at the colony level. The temporal and spatial interactions and scaling effects found, carry implications for later chapters, where I investigate colony dynamics and spatial population processes of nesting common eiders.

Chapter 4, published in the Journal of Wildlife Management (Chaulk et al. 2005b), deals with the population trend of common eiders nesting in Labrador. This chapter is straightforward in its objectives, results and conclusions. This is the first time that population trends have been evaluated for common eiders in this region. From conservation perspective the information in Chapter 4 will help identify short term research and conservation strategies. The findings in Chapter 4 also help validate past conservation efforts by local and regional management teams. In terms of its importance to the thesis, this chapter sets the stage for temporal population dynamics for eiders in this region of Labrador. Combined with my earlier findings, it aids in interpretation of overall findings presented in Chapters 5 and 6.

Chapter 5 is mechanistic and provides insight into extrinsic factors that influence eider distribution and abundance. This chapter investigates how landscape features, and ice influence patterns of abundance, incidence and dispersion; it has been submitted to *Oecologia*. The results presented in this chapter are directly related to the primary thesis question of why eiders nest where they do, and hopefully will be of use to those who wish to understand eider population processes in northern climates.

Chapter 6 is theoretically driven and assesses the colony and local population dynamics of eiders and large gulls nesting in Labrador. The main question addressed is whether eiders and gulls can be described using a metapopulation framework. Key features of metapopulations that I was interested in were local population turnover and incidence and abundance relationships.

To my knowledge no one had ever analyzed eider nesting ecology from this perspective. Chapter 6 presents empirical evidence concerning local population turnover,

structure and functioning. Local extinction and colonization patterns relate directly to conservation. I also investigated inter-specific interaction between eiders and their primary avian predators (herring and great black-backed gulls). These issues all relate directly to my primary research question of why eiders nest where they do. In the concluding chapter, I summarize my findings, and discuss future directions for research on eiders, sea ducks, colonial species, spatially structured populations, and the management implications of my thesis.

CO-AUTHORSHIP STATEMENT

Data collection on nesting eiders began in 1998 as part of a CWS population trend survey. In 2001 I began to look for a school where I might be accepted as a PhD candidate. I was accepted by MUN and officially enrolled in January of 2003. In spring of 2003 I was seconded to the Labrador Inuit Association, and I completed field work in the summer of 2003. Data analysis and manuscript writing was initiated in December 2003. With the support of my supervisors, I produced most of this dissertation by December 2004. I was primary scientist for all aspects of this project, including study design, data collection, management and analysis theoretical framing, literature research, hypothesis generation, and manuscript writing. I have produced seven chapters, including an Introduction, five research chapters and a Conclusion. I am senior author on all papers and the ideas contained is this thesis are mine, mediated by existing literature available on these subjects. However the help of the co-authors greatly enhanced the clarity, scope and focus of all chapters.

Greg Robertson is second author on all papers and deservedly so. Greg made many valuable contributions to this thesis. Mainly he acted as my primary sounding

board for theoretical and analytical ideas. He also guided me with respect to proper use of statistics, or more importantly guided me away from the improper use of statistics. He also provided timely and useful comments on all drafts of each chapter. I am indebted to him for all of his help. Bill Montevecchi is third author on most chapters (except Chapter 4). Bill acted as a sounding board for my ideas, and his greatest assistance was in pointing out ways to clarify or expand my interpretation. Bill also provided timely and useful comments on all drafts of this thesis. Bill was instrumental in my attending MUN, and without his support this thesis would not have been possible. Brian Collins was third author on Chapter 4. Brian provided the software to run the population trend analysis, but the software kept crashing at the final step of the process. To expedite data analysis, Brian, who wrote the software and had a fully functional version, agreed to run the trend analysis for me. Many thanks to him for his help in this regard. Pierre Ryan, was fourth author on Chapter 2, Pierre actually helped me establish the first of surveys in 1998 and his contribution in the field will never be forgotten. Bruce Turner was fifth author on Chapter 4, and he was instrumental in the initial establishment of the eider population trend program, and has provided me with tremendous administrative and logistical support throughout this research. I am also indebted to him for his help over the years.

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ASPECTS OF COMMON EIDER NESTING ECOLOGY IN LABRADOR

ABSTRACT: The status, distribution and nesting ecology of common eiders (Somateria mollissima) breeding in Labrador is not well known. This study is an initial effort to improve understanding of the nesting ecology of eiders on the Labrador coast, a zone of intergradation between the northern (S.m. borealis) and American (S.m. dresseri) sub-species of common eider. During 1998 and 1999, 187 islands were surveyed for nesting eiders at four sites along 750 km of the coast (from north to south - Nain, Hopedale, Makkovik, St. Peter's Bay). Nest initiation dates (calculated by candling eggs) ranged over a four to five week period and were positively associated with latitude: the earliest mean initiation date was in St. Peter's Bay (5 June) in the south and the latest in the north, at Nain (27 June). Mean clutch size ranged from 3.5 to 4.2 and varied by area and year, with eiders nesting in Nain having smallest clutches. In 1999, the highest nest density was observed in Nain with 49.8 nests/ha and the lowest in Makkovik with 3.9 nests/ha. In some cases, boat surveys were used to assess eider presence and absence and it was found to be a reliable method; this search technique could be beneficial to researchers working in remote locations where operational costs are high.

Common eiders (Somateria mollissima) are large sea ducks with a circumpolar breeding distribution (Circumpolar Seabird Working Group, 1997). They are differentiated into seven sub-species, four of which occur in North America. These sub-species show substantial variation in body size, clutch size, timing of nesting, nesting

density, migratory tendencies and other aspects of their breeding ecology (Goudie et al., 2000; Robertson et al., 2001). Two subspecies breed along the Labrador coast, S. m. borealis and S. m. dresseri. The point of demarcation between the two is generally considered to be Groswater Bay (Mendall, 1980; Goudie et al., 2000) with the range of dresseri extending southward and that of borealis northward. However, there is undoubtedly an area of overlap, and individuals showing morphometric features that are intermediate between the two subspecies (intergrades) are known to be common along the southern half of the Labrador coast (Mendall, 1980; 1986).

Very little is known about the current size of eider populations along the Labrador coast, nor about the degree of intermixture of the two subspecies and intergrades nor about population trends and nesting ecology. The goal of this paper is to document aspects of the nesting ecology of common eiders breeding at four sites along the Labrador coast. Specifically, I document clutch size, timing of nesting, and nesting density at these four sites and compare these values with eiders nesting in other parts of North America.

STUDY AREA

Archipelagos near the communities of Nain and Hopedale were surveyed during 1998 and 1999; archipelagos near the community of Makkovik and in St. Peter's Bay were also surveyed during 1999 (Figure 2.1). The archipelagos adjacent to Nain, Hopedale, and Makkovik were selected for study because they occur inside the Labrador Inuit Association (LIA) land claim area and baseline data were anticipated to form the basis of natural resource co-management between LIA and the Canadian Wildlife Service

(CWS). St. Peter's Bay was added after community groups requested it be assessed for consideration as a protected area for migratory birds.

The extent of the Nain study area was approximately 3383 km^2, it contained 1000 islands ranging in size from 0.01 – 44800 ha. The extent of the Hopedale study area was approximately 566 km^2, it contained 650 islands ranging in size from 0.01 – 3875 ha. The extent of the Makkovik study area was approximately 763 km^2, it contained 300 islands ranging in size from 0.01 – 3396 ha. The extent of the St. Peter's Bay study area was approximately 13 km^2 containing 20 islands ranging in size from 0.03-23.43 ha (Table 2.1).

All regions shared similar environmental characteristics such as a northern maritime climate, vegetation composed primarily of moss, lichen, forbe, grass, and sedge. The archipelagos of Nain, Hopedale and Makkovik were typically comprised of barren islands with sparse vegetation and very limited nesting cover. Islands in St. Peter's Bay had more ground vegetation and woody cover, such as stunted black spruce (Picea mariana). All four archipelagos are classified as coastal barrens (Lopoukhine et al., 1978), are considered to have a high-boreal ecoclimate (Meades, 1990) and a Low Arctic oceanographic regime (Nettleship and Evans, 1985).

METHODS

In all areas, islands were selected for study based on random sampling or field selection (Table 2.2). Field selection of islands was the only method used in 1998, and it was based on a haphazard selection method. However I limited searches to islands that were estimated to be smaller than 30 ha. On the first day of surveys for a community,

weather conditions were evaluated, and based on this a general direction of travel was chosen. Using direction of travel, an island cluster was chosen for sampling based on an overview of the 1:50,000 National Topographic Series (NTS) map sheets for the general area. After the first island cluster was surveyed, additional islands were chosen for sampling based on further evaluation of the NTS map sheets and an assessment of transit time. The goal was to maximize the spatial sampling distribution while balancing logistical constraints such as weather, travel distances and time. All islands were selected for survey before the study team could visually assess islands for productivity or accessibility. On subsequent days a new direction and island cluster was chosen and the method repeated. Randomly selected islands were chosen by assigning serial numbers to all islands less than 30 ha on 1:50,000 topographic map sheets. Repeat surveys of Hopedale and Nain in 1999 were conducted by randomly sampling islands selected in 1998.

Islands were accessed by powerboat and were surveyed from the water at distances of up to 7-10 m from shore for presence or absence of nesting eiders. Only small islands were searched in this manner (i.e., < 1 ha). The study team assumed nesting eiders were absent if they did not flush from the island (Nakashima and Murray, 1988; Robertson and Gilchrist, 1998; Merkel, 2004). In 1999, newly selected islands were surveyed first from boat and classed as eiders present or absent. For 30 islands classed as eiders absent, ground surveys were conducted to assess the accuracy of boat based absence classification. Islands that were searched by boat only were classed as boat searched.

Ground surveys were conducted using standard search method employed by CWS (Nettleship, 1976) and other researchers (Falardeau et al., 2003; Merkel, 2004); these

consisted of two to four people walking over the islands searching for signs of eider nesting. Islands in the three northern archipelagos were for the most part barren with limited cover; hens and unattended nests were easily detected. In several cases, nest searches were halted due to weather or logistical considerations. If searches were halted, the island was classed as partially searched. Partially searched and boat searched islands were not used in calculating the mean number of nests per island.

During 1998 and 1999, 187 different islands were searched - 113 islands in 1998 and 141 islands in 1999 (Table 2.2). Of these, 25 islands from Nain and 42 islands from Hopedale were surveyed in both years (Table 2.2). In 1998, Hopedale was surveyed from 30 June to 4 July, followed by Nain from 6 July to 10 July. In 1999, St. Peter's Bay was surveyed first from 22 June to 23 June, followed by Makkovik from 25 June to 3 July, Hopedale from 4 July to 12 July, and finally Nain from 13 July to 15 July.

For each common eider nest observed, information was recorded on apparent clutch size, nest age, and nest status (incubating, hatching, hatched, depredated, or unknown). Nests were classed as follows: incubating - current season nest containing eggs; hatching - at least 1 chick was breaking its shell; hatched - at least one chick was completely out of its shell; depredated - broken and bloody eggs were present or immediately adjacent to the nest; and unknown - nest was in disrepair with no eggs or signs of depredation (Chaulk, unpublished). Primary predators for these eiders were large gulls (Goudie et al., 2000), and occasionally evidence of mammalian predation was found. The main gull species in the study area were Great Black Backed Gull (*Larus marinus*), and Herring Gull (*L. argentatus*), Glacous Gulls (*L. hyperboreus*) are more common north of Nain, but appeared

to be less abundant and widespread than either herring or black backed gulls. It was assumed that mammals were able to access the islands using land fast ice, ice bridges and/or floating ice pans.

Nest initiation dates were estimated by candling incubating nests (Weller, 1956), and for hatching nests assuming an incubation period of 24 to 26 days (Goudie et al., 2000). The initiation date was determined by adding the number of eggs in the nest minus one to the age of the egg, assuming a laying rate of one egg/day, and incubation starting after the second or third egg (Goudie et al., 2000), and subtracting this number from the survey date. Nests with more than 6 eggs were not aged. Apparent clutch sizes were calculated using only nests classified as incubating; nests with more than 6 eggs are generally considered dump nests produced by two or more females (Swennen, 1983; Robertson, 1995) and were therefore omitted from the analysis. Island nest counts and nest density were calculated based on islands that were completely searched. Island sizes were based on GIS analysis of digital 1:50000 maps for the coast of Labrador. Geodetic coordinates are reported as Latitude and Longitude, decimal degrees, North American Datum 1983. Nest initiation, nest counts, nest density and clutch size data collected in 1999 were analyzed using One-way ANOVA with community as the only factor in the model, and critical alpha was set at 0.05 for all tests.

RESULTS

In 1998, 113 islands were searched and 720 eider nests were counted, overall there were 6.6 nests/island or 14.3 nests/ha (Table 2.3). In 1999, 141 islands were searched and 1439 eider nests were counted, on average there were 12.6 nests/island or

18.0 nests/ha (Table 2.3). Makkovik had the lowest percentage of islands with eiders present, followed by Hopedale, Nain, and St. Peter's Bay (Table 2.2).

Islands in Nain and Hopedale that were surveyed in both 1998 and 1999 were analyzed for differences in nest counts using the General Linear Model. For islands searched in 1999, the number of nests/island differed significantly between areas ($F = 14.45$; $df = 3, 110$; $p < 0.01$), with the highest nest counts in St. Peter's Bay followed by Nain, Hopedale and Makkovik (Table 2.3). In 1999 nest density also varied by region ($F = 3.44$; $df = 3, 110$; $p = 0.02$). The highest nest densities were observed in Nain, followed by St. Peter's Bay, Hopedale, and Makkovik (Table 2.3).

In 1998, 7.5% of found nests were depredated, while in 1999 3.3% of nests were depredated (Table 2.3). The highest level of hatched and hatching nests was observed in 1999 in St. Peter's Bay followed by Hopedale. Nest initiation date varied by region in 1999 ($F = 95.97$; $df = 3, 154$; $p < 0.01$) with nest initiation occurring earliest in St. Peter's Bay in the south, followed by Makkovik, Hopedale, and Nain (Table 2.3). Mean nest initiation date for Hopedale and Nain was approximately the same in both 1998 and 1999. Clutch size varied by region in 1999 ($F = 3.25$; $df = 3, 944$; $p = 0.02$) with the smallest clutch size occurring in Nain and the largest in Hopedale (Table 2.3). In 1999, islands were assessed by boat and classed as eiders absent; 30 of these were then surveyed on foot to verify the absence classification, all 30 were verified as eiders absent.

DISCUSSION

According to accounts by local residents during the 1998 and 1999 surveys, spring break up and subsequent transition, the timing and onset of spring and summer

were typical for all study areas. Overall, the surveys appeared to be well timed as most nests were incubating (≥80% for 4 of 6 survey areas; Table 2.3) except in 1999 at St. Peter's Bay and Hopedale, when I observed a higher percentage of hatched nests.

The method of assessing small islands by boat to see if eiders were present and classifying them as unoccupied if none flushed has been used before (Nakashima and Murray, 1988; Robertson and Gilchrist, 1998; Merkel, 2004). Avoiding landings on islands that do not have nesting birds can significantly speed up survey times and reduce survey effort. However this technique had yet to be verified. In this study 30 islands were classified as unoccupied based on boat surveys, these islands were subsequently assessed on foot and in all cases no eider nests were found. I do caution other researchers however, and suggest that they employ a similar verification technique for individual study areas and not to use this method when investigating larger islands.

St. Peter's Bay in southern Labrador had the earliest average nest initiation date (5 June) of any area surveyed. In Labrador, nest initiation date was positively associated with latitude, and is likely related to the timing of spring ice break-up (Goudie et al., 2000). Ice may affect the timing of nest initiation for many reasons, including obscuring of food resources, increased predator access, or by simply being correlated with colder local conditions. Another factor that might influence nest initiation is subspecies affiliation. I found that nest dates were similar during 1998 and 1999 in both Hopedale and Nain, occurring in mid to late June. Eiders nesting in Labrador showed relatively late nest initiation dates and subsequent hatching dates compared to some eider populations. Peak nest initiation for S. m. dresseri nesting in the St. Lawrence estuary

occurred during the 3rd week of May (van Dijk, 1986) and for S. m. sedentaria populations breeding in western Hudson Bay, at a similar latitude as Labrador, peak nest initiation was in late May (Robertson, 1995). The results are more comparable to S. m. borealis populations, such as those nesting in southern Baffin Island (Cooch, 1965), Devon Island (Prach et al, 1986) and Ungava Bay (Falardeau et al., 2003), or S. m. sedentaria populations breeding in eastern Hudson Bay (Freeman, 1970), which all show peak nest initiation dates ranging from mid-June to early July.

There were statistically significant differences in clutch size among regions in 1999. The largest average clutch size was observed in Hopedale, while the smallest was observed in Nain. Mean clutch sizes for S. m. borealis vary from 3.3-3.6 eggs (summarized in Robertson et al., 2001), although Falardeau et al. (2003) reported clutch sizes ranging as low as 2.0 to 2.9 eggs per nest for S. m. borealis nesting in Ungava Bay in 2000. Mean clutch sizes for S. m. dresseri vary from 3.6-4.4 while S. m. sedentaria show larger clutch sizes ranging from 4.0-4.4 eggs (Robertson et al., 2001). The clutch sizes I observed in Labrador were generally higher than the usual range for S. m. borealis, but within the range normally seen for S. m. dresseri.

Nest densities were highly variable among regions, with some regions showing dispersed nesting, and others, such as Nain, showing relatively dense breeding. Makkovik had the lowest ratio of eiders present on islands and the lowest nest densities. It is unclear why this pattern arose, as island nest density and archipelago island density did not appear to be related. Nest densities in other subspecies are highly variable as well; nest densities for S. m. dresseri in the Gulf of St. Lawrence averaged 3 nests/ha, while

colonies in the estuary reached 741.5 nests/ha (Chapdelaine et al., 1986). Typically, S. m. borealis exhibits low nesting densities, but there are some notable exceptions, such as East Bay, Southampton Island. S. m. sedentaria populations showed slightly lower or similar nest densities as Labrador breeders, ranging from 1.0–15.9 nests per island (Nakashima and Murray, 1988; Robertson and Gilchrist, 1998). Nesting densities in all common eiders subspecies are likely to be related to a variety of interacting local factors, including, but not limited to, available nesting islands and brood rearing areas, predator numbers, and population density.

Common eiders breeding along the Labrador coast show some traits similar to S. m. borealis, such as late nest initiation, but also show large clutch sizes, which are more typical of S. m. dresseri (Robertson et al., 2001). However, characteristics such as nest initiation could also vary due to environmental factors such as timing of spring break-up. Since Labrador eiders have been shown to be intergrades between two subspecies (Mendall, 1980, 1986) and show intermediate nesting ecology, and for management purposes I suggest that they be considered separately from other populations. Future research on common eiders in Labrador should include the development of population trends, population genetics, identification of wintering areas, and an assessment of biophysical factors influencing breeding distribution and abundance.

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Table 2.1 Summary of study area extent, island count, total island area and island size.

Study Area	Nain	Hopedale	Makkovik	St. Peter's Bay	Total
Extent (km^2)	3383	566	763	13	4725
Number of Islands	1000	650	300	20	1970
Islands/km^2	0.29	1.15	0.39	1.54	0.42
Mean Island Size (ha)	113.3	22.0	27.6	3.2	41.5
sd island size (ha)	1602.7	205.3	219.5	5.7	748.2

Table 2.2 Summary of island sampling method, search status, and island size by survey area during 1998 and 1999.

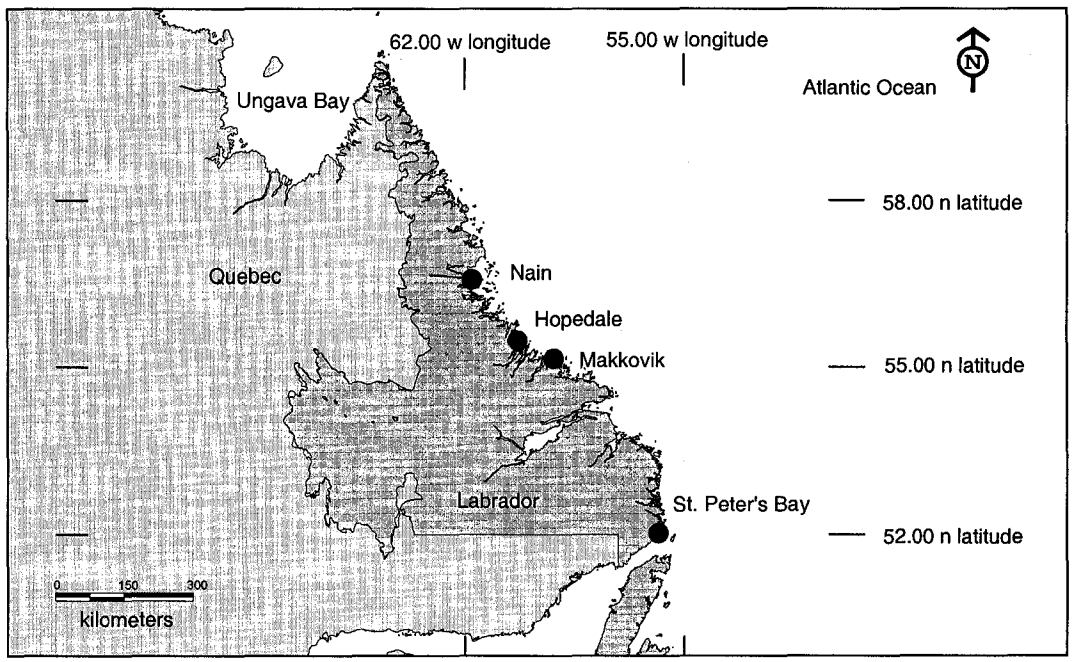
	Nain		Hopedale		Makkovik	St. Peter's Bay	Total		
	1998	1999	1998	1999	1999	1999	1998	1999	All
Method									
Field Selection	43	5	70	6	22	10	113	43	156
Random	0	10	0	0	21	0	0	31	31
Repeated	0	25	0	42	0	0	0	67	67
Survey									
Total	43	40	70	48	43	10	113	141	254
Search Status									
Complete	43	31	66	46	27	10	109	114	223
Partial	0	1	4	0	2	0	4	3	7
Boat	0	8	0	2	14	0	0	24	22
Total	43	40	70	48	43	10	113	141	254
Isl. Size (ha)[+]									
Total Area	81.4	34.1	188.2	140.5	73.4	56.8	269.6	304.8	574.4
Mean	1.9	1.1	2.9	3.0	2.7	5.7	2.5	2.7	2.6
Sd	2.4	1.1	6.5	7.2	3.2	7.1	5.3	5.4	5.4
Min	0.04	0.07	0.07	0.07	0.15	0.39	0.04	0.07	0.04
Max	12.1	4.9	46.1	46.1	13.4	23.4	46.1	46.1	46.1
N	43	31	66	46	27	10	109	114	223
% eiders present	74	60	50	60	34	80	59	54	57

[+] based on islands that were completely searched.

Table 2.3 Summary of Nest initiation, Clutch size, Nest counts, Nest density, and Nest status by survey area during 1998 and 1999.

	Nain		Hopedale		Makkovik	St. Peter's Bay	Total		
	1998	1999	1998	1999	1999	1999	1998	1999	All
Nests/Island									
Mean	12.3	20.3	2.9	4.3	4.0	50.6	6.6	12.6	9.9
Sd	18.1	26.2	6.6	7.7	9.9	56.3	13.2	25.9	26.1
complete search	43	31	66	46	27	10	109	114	223
Nests/ha									
Mean	29.8	49.8	4.2	5.1	3.9	17.3	14.3	18.0	16.2
Sd	105.2	124.0	9.7	10.9	10.4	18.0	67.2	67.6	67.6
complete search	43	31	66	46	27	10	109	114	223
Status (%)									
Incubating	80.3	79.8	87.3	65.8	91.5	43.3	82.2	65.9	71.3
Hatched	1.3	0.8	1.1	5.5	0.0	31.0	1.3	12.0	8.4
Hatching	0.2	1.1	0.0	4.5	0.0	4.3	0.1	2.6	2.0
Depredated	8.1	3.0	5.8	7.0	0.0	3.4	7.5	3.5	4.8
Unknown	10.2	15.3	5.3	17.1	8.5	18.0	8.9	16.0	13.5
N	532	628	189	199	106	506	720	1439	2159
Nest Initiation									
Mean (date)	27/06	28/06	20/06	20/06	18/06	5/06	24/06	18/06	20/06
sd (days)	5.0	6.1	5.4	6.6	6.5	7.0	6.3	11.0	14.2
N	217	52	142	46	19	41	359	158	517
Clutch Size									
Mean	3.7	3.7	4.4	4.0	3.9	3.8	3.9	3.8	3.8
Sd	1.5	1.4	1.4	1.2	1.3	1.1	1.5	1.3	1.4
N	427	501	165	131	97	219	592	948	1540

Figure 2.1. Map of general location of communities adjacent to each study area (black dots) on the Labrador coast in 1998 and 1999.



CHAPTER TRANSITION

In this chapter I investigated whether spatial variation existed for reproductive parameters such as nest initiation date, clutch size, nest density, of nesting eiders along the entire coast of Labrador. I found significant variation in all traits, and a trend of more northern traits (smaller clutches and later nesting) at more northern sites. This finding indicates that some spatial structuring is occurring along the Labrador coast, at least in reproductive traits. In the next Chapter I look at similar reproductive parameters but investigate in more detail how spatial and temporal variations interact. Understanding how patterns in space are influenced by variation across time is fundamental to our overall understanding of distribution processes. Without this understanding, variation may be mistakenly assigned as spatial when in fact it is temporal variation occurring independently at different sites.

REGIONAL AND ANNUAL VARIABILITY IN COMMON EIDER NESTING ECOLOGY IN LABRADOR

ABSTRACT: Nesting densities are often used to estimate breeding population size and with other measures of reproductive performance can be useful indicators of population status. These aspects of breeding biology often show considerable spatial and temporal variation. To assess the extent of this variation, between 2000-2003, I surveyed nesting common eiders (*Somateria mollissima*) on 172 islands in three archipelagos (Nain, Hopedale, Rigolet) on the coast of Labrador. Over the course of this study I counted 12,256 nests, and recorded nest initiation date, nest density, egg volume, clutch volume and clutch size. Island density varied inversely with the size of the archipelago; Rigolet was the largest archipelago (2834 km^2) followed by Nain then Hopedale, which had the highest island density (0.90 islands/km^2). Overall means were 52.0 ± 141.9 (SD) nests/ha; 13 June ± 12 days; 3.7 ± 1.2 eggs/nest; 98.8 ± 10.4 cm^3 for egg volume and 392.3 ± 135.0 cm^3 for clutch volume. Rigolet had the highest nest densities and egg volumes and the highest single island nest density of 1,053 nests/ha, and the earliest nest initiation dates. I found significant differences in nest densities among archipelagos and across years; significant archipelago by year interaction was detected for nest initiation date and clutch size. Only one year of data was available for egg volume, but there was a significant difference in egg volume among the three archipelagos. Significant differences were found among individual islands for all response variables except egg volume. Egg volume did not show small scale local variation, but did show large-scale regional variation, and

may be a meaningful breeding characteristic that can be used to identify population affiliation, however I was not able to test year effects, and are not sure how egg volume varies with time. Long-term comparative studies of eider nesting ecology on the Labrador coast may facilitate better understanding of avian responses to environmental and human induced perturbation and change.

Understanding regional and annual variation in the breeding ecology of organisms is important for conservation and management purposes. Variable expression of ecological characteristics often occurs in response to change in the environment where organisms live. Breeding ecology can be influenced by biophysical factors at differing temporal and spatial scales (Scott et al. 2002). Aspects of avian ecology such as nest density, clutch size, and egg volume can be influenced by population dynamics, habitat quality, and/or food availability (Lack 1967; Ryder 1970; Hario & Selin 2002). Furthermore some components of breeding ecology may be prone or resistant to annual and/or regional fluctuations in the biophysical environment (Avise & Hamrick 1996; Erikstad et al. 1998; Bregnballe 2002; Hario & Selin 2002).

Common eiders (*Somateria mollissima*) are an important species for many northern peoples, as a source of meat, eggs and down. These birds exhibit substantial variation in the timing of nesting, nesting density, clutch size and other aspects of their breeding ecology (Goudie et al. 2000; Robertson et al. 2001; Chaulk et al. in press). Understanding patterns of annual and regional variation in eider breeding performance can be very important for management and conservation purposes. Early nest initiation

dates, and large clutch sizes are generally indicative of favourable breeding conditions, while nesting densities are often used to estimate breeding population size. Unfortunately most eider research is limited in spatial and/or temporal scope, and the rare papers that contain multi-year and/or multi-site comparisons, are from temperate and northern Europe (Milne 1974; Swennen 1983; Coulson 1984, 1999; Hario and Selin 1988; Bregnballe 2002; Hanssen et al. 2003).

The goal of this paper was to examine annual and regional variation of common eider, nesting ecology at three distinct sites on the northern Labrador coast, a subarctic region, over a four-year period (2000 to 2003). In this paper, I investigate nest density, clutch size, and nest initiation in three archipelagos across four years and examine regional patterns of egg and clutch volume. Generally speaking I expected differences between archipelagos and year with respect to most breeding characteristics, however I had limited prior understanding of how these differences would vary with respect to their magnitude and direction when the effects of space and time were modeled together.

STUDY AREA

Archipelagos near the communities of Nain, Hopedale and Rigolet were surveyed from 2000 to 2003 (Figure 3.1). The extent of each archipelago was determined by calculating a Minimum Convex Polygon (Mohr 1947) containing all islands that were completely searched. The total geographic area of the three archipelagos was estimated to be 4785 km^2, and contained approximately of 1600 islands (Table 3.1). The archipelago adjacent to Rigolet covered the largest geographic area while the archipelago adjacent to Hopedale was the smallest (Table 3.1). Overall the average size of islands

within the three archipelagos was 30.1 ha ± 288.8 (1 SD), on average the largest islands were found in the Rigolet archipelago (Table 3.1). The greatest island density occurred in the Hopedale archipelago (0.90 islands/km^2) followed by Nain then Rigolet (Table 3.1).

All archipelagos shared similar environmental characteristics such as a northern maritime climate, vegetation composed primarily of mosses, lichens, forbes, grasses, and sedges. The archipelagos were typically comprised of barren islands with sparse vegetation and very limited nesting cover. Islands in the Rigolet area had denser and taller ground vegetation, and on some islands more shrub cover, including stunted black spruce (*Picea mariana*). All three archipelagos are classified as coastal barrens (Lopoukhine et al. 1978), are considered to have a high-boreal ecoclimate (Meades 1990) and a Low Arctic oceanographic regime (Nettleship & Evans 1985). Meanwhile the reader should be aware that the concept of discrete archipelagos somewhat misleading, as the island complex which occurs along the Labrador coast is typically continuous. Within the section of Labrador that I report in this paper, the island complexes described above, hereafter referred to as archipelagos, are typical for this region.

METHODS

From 2000 to 2003 I surveyed three archipelagos (Nain, Hopedale, Rigolet) for nesting eiders. Islands were selected for study on the basis of random sampling. In all cases I limited searches to islands that were estimated to be smaller than 30 ha. Analysis of the spatial distribution of my data set show that my samples were spatially random within the subset of islands that were less than 30 ha within each archipelago (Chaulk unpublished data). Ground surveys were conducted using standard search method

employed by the Canadian Wildlife Service (Nettleship 1980) and other researchers (Falardeau et al. 2003; Merkel 2004; Chaulk et al. in press); these consisted of two to four people walking linearly over the islands searching for signs of eider nesting. Islands in the three archipelagos were typically barren with limited nest-cover; hens and unattended nests were easily detected. Archipelagos were searched at approximately the same time each of the four years (Table 3.1). Typically the senior author conducted all surveys. The exception being Nain and Hopedale in 2001 and 2002, where the senior author initiated the surveys but the field crew completed the surveys.

For each common eider nest observed, information was recorded on apparent clutch size, nest age, and nest status (incubating, hatching, hatched, depredated, unknown). Nests were classed as follows: incubating - current season nest containing eggs; hatching - at least 1 chick was breaking its shell; hatched - at least one chick was completely out of its shell; depredated - broken and bloody eggs were present or immediately adjacent to the nest; and unknown - nest was in disrepair with no eggs or signs of depredation (Chaulk et al. in press).

Although recent research suggests that the start of incubation is related to the laying on the penultimate egg (Hanssen et al. 2002), therefore one might expect variation between different clutch sizes. For this paper the incubation period was assumed to be approximately 24 to 26 days, with incubation generally commencing after the second or third egg has been laid, with hens laying about 1 egg per day (Goudie et al. 2000). Candling was used to age the eggs (Weller 1956) and to calculate nest initiation I added the number of eggs to the egg age and I subtracted this number from the survey date. Nests

with more than 6 eggs were not aged. Apparent clutch sizes were calculated using nests classified as incubating; nests with more than 6 eggs are generally considered dump nests produced by two or more females (Swennen 1983; Robertson 1995) and were omitted from the analysis.

In 2003, a random number table was used to randomly select a subset of previously surveyed islands. On these islands a die toss was used to randomly select nests with one or more eggs. For example, rolling a two meant I checked every second nest until I had a minimum of 6 measurements per island. The same die was used to randomly select a single egg from each nest. For example, I only measured eggs where clutch sizes was < six eggs, I assigned each egg a number and then rolled the die. The randomly selected egg was then measured using Vernier calipers, egg length was measured from pole to pole, and width was measured at the widest part of the egg, all measurements were recorded in mm. Egg volume was calculated based on the formula presented by Guild (1974) and Robertson et al. (2001), clutch volume was estimated only for nests for which I had data on egg volume and clutch size. Clutch volume was estimated as clutch size multiplied by the estimated egg volume for a given nest.

Island nest densities were calculated using islands that were completely searched. Island sizes were derived from digital 1:50000 base maps for the Labrador coast. Geodetic coordinates are reported as Latitude and Longitude, decimal degrees, North American Datum 1983.

Nest density, nest initiation, and clutch size were analyzed using a General Linear Model, with the year, archipelago and its interaction as fixed factors. Island, nested

within archipelago, was also included as a random factor to control for multiple measurements of islands across years. Egg volumes and clutch volumes were analyzed with one-way ANOVA, with archipelago as a fixed factor and island, nested within archipelago, as a random factor. Critical alpha was set at 0.05 for all tests, which were all two-tailed.

RESULTS

I sampled 172 islands in the three archipelagos with the greatest island sampling effort expended in Hopedale (Table 3.1). The average size of sampled islands was 2.3 ± 6.0 ha (Table 3.1). On the islands that were completely searched I counted 10,962 eider nests and these contained 35,401 eggs. Overall, on average there were 52 nests/ha or 172 eggs/ha (Table 3.2). The highest nest counts were observed in Rigolet; one island had 654 nests, and a different island 0.18 ha in size, had the equivalent of 1053 nests/ha. For island nest-density both community and year were significant factors, although they did not show statistically significant interaction (Table 3.3). There appeared to be greater regional variation than annual variation in nest density (Figure 3.2).

The overall average nest initiation date was 13 June, the earliest average nest initiation dates occurred in the south at Rigolet (4 June) and the latest in the north at Nain (24 June) (Figure 3.4), however I detected a significant interaction between community and year for nest initiation date (Table 3.3, Figure 3.3). The overall average clutch size was 3.7 ± 1.2 eggs/nest (Table 3.2). The largest average clutch size was observed in Hopedale at 3.8 ± 1.2 eggs, followed by Rigolet at 3.7 ± 1.2 eggs, and Nain at 3.6 ± 1.2 eggs, however I detected a significant interaction between community and year for clutch

size (Table 3.3, Figure 3.4). Nests with more than 6 eggs were omitted from the clutch size calculation. In all three archipelagos over the four year period of this study I counted 210 nests with seven or more eggs (Table 3.4). Egg volume varied significantly among archipelagos but not across individual islands (Table 3.3), the largest egg volume was observed in Rigolet and the smallest in Nain (Figure 3.5). The largest clutch volume was observed in Hopedale (Figure 3.5) although the differences among archipelagos were not significant (Table 3.3).

DISCUSSION

The highest nest density that I observed occurred in Rigolet (1053 nest/ha), this observation was made on a small island approximately 0.18 ha, and is high relative to nest densities reported elsewhere. Overall, average nest density was 52.0 nests/ha. *S. m. borealis* typically nest at low nest densities, though there are some exceptions, such as East Bay, Southampton Island (Abraham & Finney 1986). Nest densities for *S. m. dresseri* in the St. Lawrence River averaged 3 nests/ha, but reached as high as 741.5 nests/ha (Chapdelaine et al. 1986). Nesting densities are probably influenced by numerous interacting local factors, including, but not limited to, available nesting islands and brood rearing areas, predators, disturbance, and overall population size.

I also observed significant differences in nest densities among archipelagos across a larger geographic range in Labrador, but were not able to examine annual variation (Chaulk et al. in press). The present analysis suggests that annual variation is important, and suggests increasing nest densities over the 2000-2003 study period.

The timing of spring ice break-up was late in both the Hopedale and Nain archipelagos during 2002. I found a significant interaction between archipelago and year with respect to nest initiation date, with Rigolet in the south showing relatively consistent timing, and the two northern archipelagos showing more annual variation.

Earlier, I documented that nest initiation dates in Labrador were positively related to latitude, but I was not able to test year effects (Chaulk et al. in press). This latitudinal pattern still holds over multiple years, though Nain in the north showed the latest initiation dates in only two of the four study years. This discrepancy with my earlier paper highlights the importance of multi-year studies, especially for those aspects of breeding ecology that can be easily influenced by biophysical factors, such as sea ice break-up in the spring (Laurila & Hario 1988; Goudie et al. 2000). Given that I found an interaction between archipelago and year in nest initiation date, it is likely that nest initiation date is influenced by ice conditions at the local level. It is important to recognize that common eider nest initiation can be influenced by annual variation in the timing of spring break-up. This could mean that common eiders are a good species for monitoring the effects of climate change in this region of North America, but my results show that more than one site would need to be monitored.

Clutch size is often used as a comparative measure between different populations (Lewis 1939; Milne 1974; Swennen 1983; Coulson 1984; Robertson et al. 2001; Bregnballe 2002; Chaulk et al. in press). Common eider clutch size is influenced by female body condition, food availability, disease, body parasites, winter severity, timing of spring, predation, and nest parasitism (Rohwer 1992, Erikstad et al. 1993), and some

researchers have suggested that average clutch size may increase during population growth (Hario & Selin 1988), while other have found no such trend (Swennen 2002).

My analysis revealed a significant interaction of archipelago and year on clutch size, indicating that any annual patterns were not matched across regions. However, my model had a low R^2 value, therefore a significant amount of variability remains unexplained by either archipelago, year or their interaction. Interestingly, Bregnballe (2002) did find that clutch size varied across years in a similar way across 5 colonies in Demark. While at a larger spatial scale, Coulson (1999) found that clutch size varied independently across years between Scottish and Dutch colonies. Clearly, the geographic scale of the analysis appears to be important. Previously, I found significant archipelago differences in clutch size but this finding was based on analysis of one year of data (Chaulk et al. in press). Annual and regional variation in clutch size is not surprising. My new findings suggest that average clutch size varies by archipelago and year at the scale of coastal Labrador, and I do not recommend the use of single measures (i.e., one archipelago and/or year) of clutch size as a basis to assess population productivity. Instead long-term measurements over many archipelagos are needed for robust comparisons between different populations.

Some studies have shown that annual variation in eider egg volume is limited (Swennen & van der Meer 1992; Robertson 1995; Laurila & Hario 1998; Hanssen et al. 2002). As such, egg volume may hold value as a comparative measure between populations at large geographic scales (Robertson et al. 2001). In 2003, egg volume differed significantly by archipelago, but not by island, whereas clutch volume differed

by island but not by archipelago. Clutch volume is largely influenced by clutch size, and likely has limited value as a comparative measure between archipelagos (see above). My data support the idea that average egg volume has merit to assess population structure at moderate geographic scales (i.e., 100's of km). But with only one year of data it is still necessary to measure annual variation in egg volume to assess spatial and temporal interaction.

Using values presented in Goudie et al. (2000) I calculated average egg volumes for two subspecies of common eiders in North America (*borealis* = 96.35 ± 4.36, range = 93.8 – 102.8; *dresseri* = 107.95 ± 5.46, range = 100.6 – 115.8). Based on an examination of these values it appears that egg volumes from Nain were most similar to those of *borealis*, while the values for Hopedale and Rigolet where on the high end for *borealis* and on the low end for *dresseri*. This pattern is likely the result of intergradation between *borealis* and *dresseri* in the zone of overlap that is considered to occur in both Hopedale and Rigolet (Mendall 1980; Chaulk et al. in press). Egg volume did follow a latitudinal pattern with eiders from Rigolet in the south having the largest egg volumes and eider from Nain in the north having the smallest.

Finally, I feel the need to comment on my sampling scheme, as the average size of sampled islands was significantly lower than the average size of islands in each archipelago. I actively excluded islands larger than 30 ha from my surveys. I did this for logistical reasons, as large islands require significant effort to search, so instead I focused on smaller islands that could be easily censused by small field crews over restricted time periods. Goudie et al. (2000) reported that common eiders preferred nesting on islands <

75-100 ha. Other researchers have used island size thresholds to help identify islands for investigation during eider breeding research (Nakashima & Murray 1988; Robertson & Gilchrist 1998; Merkel 2004) or focused on small islands during breeding surveys (Korschgen 1977; Gotmark & Ahlund 1984). It is possible that omitting islands > 30 ha have impacted my results, most likely with respect to my estimates of nest density and percentage of occupied islands. In addition, larger islands might have greater vegetative coverage, and cover has been shown to increase nest success (Choate 1967; Milne 1974; Schmutz et al. 1983), in turn nest success could impact some of the breeding characteristics that I discuss in this paper. However, since I lack data from islands > 30 ha I have no way of knowing the magnitude or direction of these differences. Meanwhile, I recognize that the spatial structuring and the biophysical characteristics of eider breeding islands are important, I feel these variables are beyond the scope of this paper and I hope to investigate the spatial ecology and habitat requirements of common eiders breeding in Labrador in future research.

CONCLUSIONS

To summarize my findings, when annual effects were detected, they often interacted with regional effects. Based on the inter-annual and inter-regional variation, as well as their interactions, long-term surveys over wide geographic regions are needed for comprehensive understanding of population dynamics and responses to environmental changes on which sound management decisions can be developed. For example, high clutch sizes and early breeding could lead to a liberalization of hunting regulations given the expected large number of young birds in the fall flight. Conversely, reduced clutches

and late breeding might be used as rational to reduce harvest quotas and seasons. However, if only one site was assessed, my results suggest that these indicators of breeding conditions would not be representative for an entire breeding range. Finally, egg volume does not appear to vary between islands at small geographic scales (i.e., within an archipelago), but does vary at moderate geographic scales (i.e., 100's of km's) and could hold promise as an indicator of population genetic differences (Robertson et al. 2001).

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Table 3.1. Location, island characteristics, sampling intensity and sampling dates of archipelagos in Labrador where nesting ecology data was collected for common eiders (*Somateria mollissima)*, 2000-2003.

	Nain	Hopedale	Rigolet	All
Study Area Location				
Mean Longitude (°W)	-61.06	-59.81	-57.41	
Mean Latitude (°N)	56.36	55.33	54.18	
Study area size (km^2)	1151	800	2834	4785
Study area perimeter (km)	145	128	278	551
N (Islands) in study area	497	720	335	1552
Island density (islands/km^2)	0.43	0.90	0.12	0.32
Archipelago Island size				
mean ± 1 SD (ha)	33 ± 318	20 ± 194	47 ± 394	30 ± 289
Range (ha)	0.01-6903	0.02-3875	0.02-5204	0.01-6903
Size sampled islands				
Mean ± 1 SD (ha)	1.3 ± 1.5	1.6 ± 2.6	4.1 ± 10.2	2.3 ± 6.0
Island Sampling Scheme				
No. one year only	13	33	17	63
No. two years only	11	19	15	45
No. three years only	10	14	12	36
No. four years only	8	13	7	28
Survey Dates 2000	3 - 9 July	28 - 30 June	20 - 26 June	20 June – 9 July
Survey Dates 2001	5 – 19 July	4– 17 July	18– 27 June	18 June - 19 July
Survey Dates 2002	13– 22 July	3– 17 July	17 - 22 June	17 June – 22 July
Survey Dates 2003	11– 13 July	3– 7 July	14– 20 June	14 June – 13 July

Table 3.2. Mean (± 1 SD) and ranges of nesting traits of common eiders breeding in Labrador, 2000-2003.

	Period	N	Mean
Nest Density (nests/ha)	2000-03	331	52.0 ± 141.9 (range = 0 - 1053)
Nest Initiation	2000, 02-03	272	12 June ± 12 d (range = 21 May to 9 July)
Clutch Size	2000-03	10137	3.7 ± 1.2 (range = 0 - 6)
Egg Volume (cm^3)	2003	415	98.8 ± 10.4 (range = 61.0 = 160.0)
Clutch Volume (cm^3)	2003	415	392.3 ± 135 (range = 77.2 = 1008.4)

Table 3.3. Summary of General Linear Model analysis by variable for nesting characteristics of common eiders breeding in Labrador, 2000-2003.

Variable	Model Fit R^2-adjusted (%)	Factors	df	F	p
Nest Density	90.3	Year	3	4.2	< 0.01
		Archipelago	2	3.9	0.02
		Year Archipelago Interaction	6	1.1	0.36
		Island nested in Archipelago	165	17.9	< 0.01
Nest Initiation	72.6	Year	2	42.7	< 0.01
		Archipelago	2	62.1	< 0.01
		Year Archipelago Interaction	4	7.1	< 0.01
		Island nested in Archipelago	63	2.4	< 0.01
Clutch Size	6.6	Year	3	3.5	< 0.01
		Archipelago	2	9.4	0.01
		Year Archipelago Interaction	6	10.1	< 0.01
		Island nested in Archipelago	116	4.7	< 0.01
Egg Volume	6.1	Archipelago	3	5.5	< 0.01
		Island nested in Archipelago	43	1.1	0.27
Clutch Volume	11.5	Archipelago	3	0.8	0.44
		Island nested in Archipelago	43	2.0	< 0.01

The reader should note that in the Factors column, the word nesting refers to syntax and model structure specific to the statistical testing (Sokal and Rohlf 1995) and not a breeding characteristic.

Figure 3.1. General location of archipelagos surveyed between 2000-2003 on the Labrador coast.

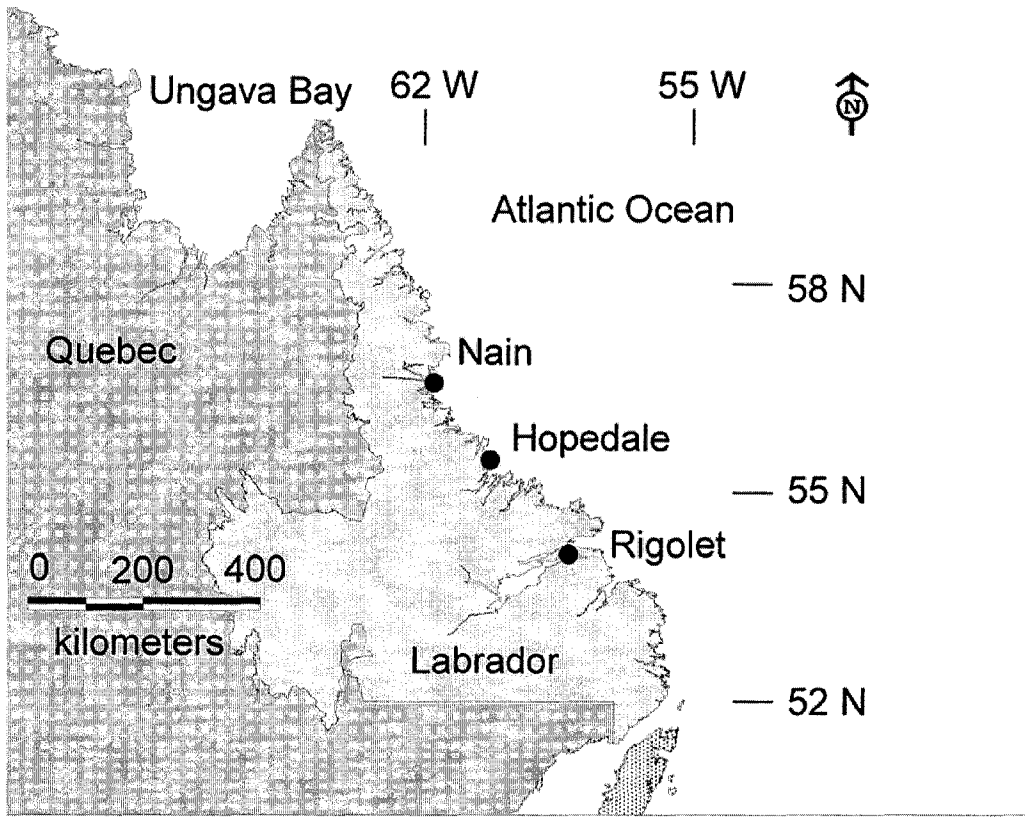


Figure 3.2. Interval plot of mean nest density (nests/ha) by archipelago and year with 95% CI. Horizontal line is equal to the overall mean.

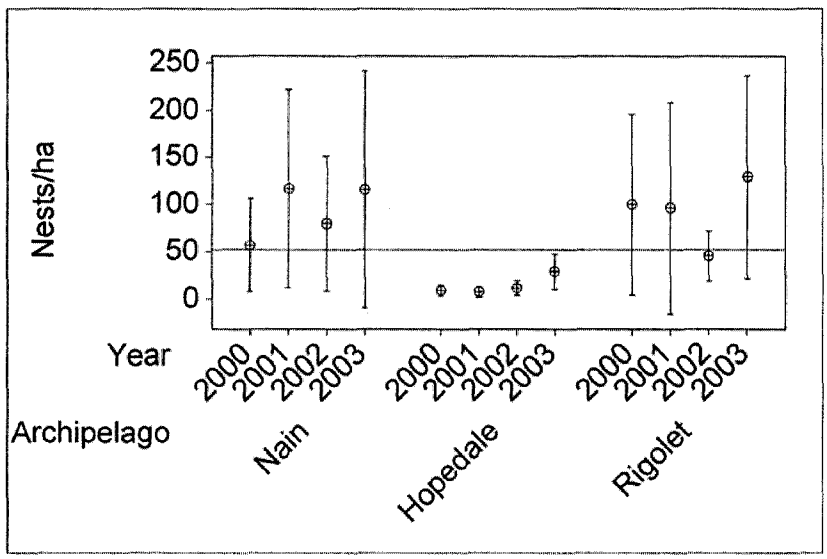


Figure 3.3. Interaction plot of mean nest initiation (day of year) by archipelago and year. Horizontal line is equal to the overall mean.

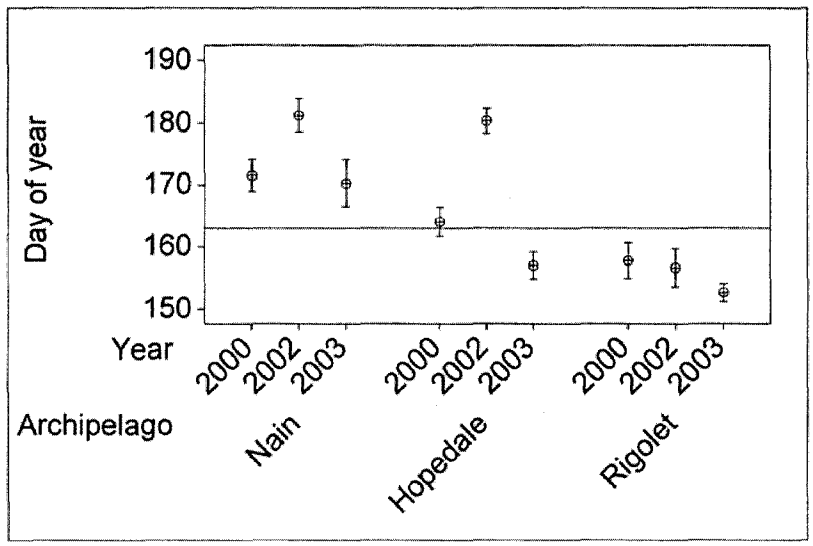


Figure 3.4. Interaction plot of mean clutch size (eggs/nest) by archipelago and year. Horizontal line is equal to the overall mean.

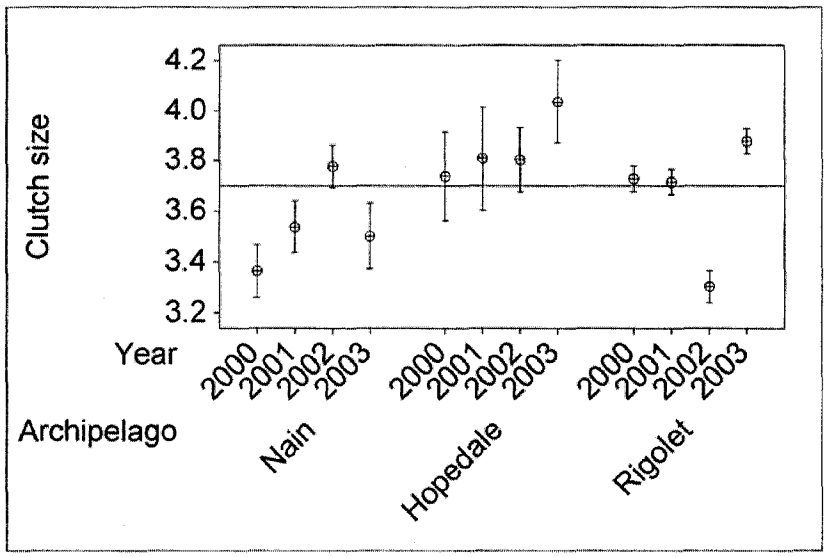
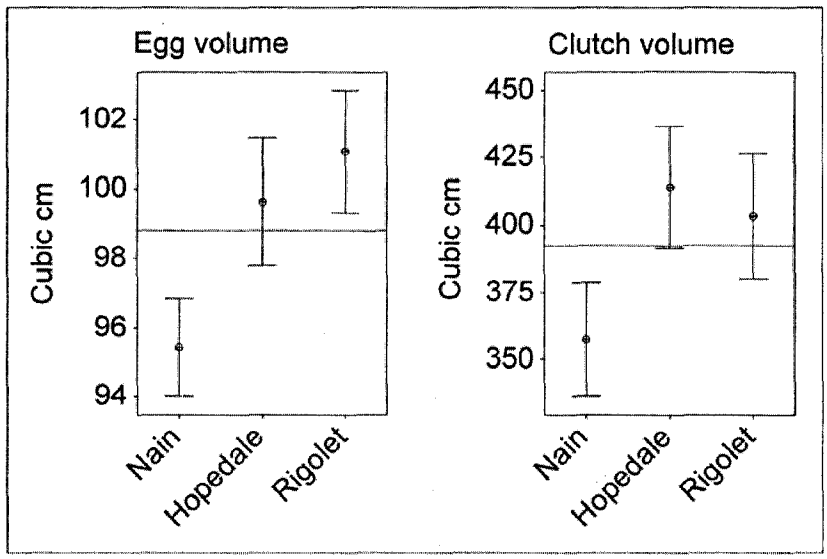


Figure 3.5. Interval plot of mean egg and clutch volume (cm^3) by archipelago with 95% CI. Horizontal lines are equal to the overall means.



CHAPTER TRANSITION

In this chapter I found that significant temporal and spatial variation occurred in nesting traits of eiders in Labrador. These findings also demonstrate that short term studies of eiders, and probably many marine birds, may not capture regional and temporal interactions, this may in turn influence data interpretation. Along with Chapter 2, I have shown that some important correlates of fitness (clutch size and nest initiation dates) and nest density vary across time and space, these correlates of fitness may in influence the distribution and abundance of nesting eiders. This is important basic information that will aid our overall understanding of eider distributions.

In the next Chapter I focus in detail on temporal changes in abundance from 1998-2003, while considering regional differences in these changes. As with the previous two chapters, Chapter 4 aids our overall understanding of the status and trends of nesting eiders in Labrador, which will aid wildlife managers. More importantly, Chapter 4 is the first step in this thesis toward understanding important large scale population processes over time.

EVIDENCE OF RECENT POPULATION INCREASES IN COMMON EIDERS BREEDING IN LABRADOR

Populations of several sea ducks are declining across their North American ranges (Sea Duck Joint Venture Management Board 2001), including populations of all 4 eider species (*Somateria* spp. and *Polysticta steller;* Kertell 1991, Stehn et al. 1993, Gratto-Trevor et al. 1998). Declines in common eider populations have been documented in Greenland, Hudson Bay, and Alaska (Robertson and Gilchrist 1998, Sudyam et al. 2000, Merkel 2004). Reasons behind these population decreases vary and many are unclear. Factors identified as causing these declines include human disturbance, over-harvesting, and climatic events (Robertson and Gilchrist 1998, Suydam et al. 2000, Merkel 2004). However, not all common eider populations in the north are decreasing; Christensen and Falk (2000) recently found evidence of population increase in an eider population in Northwest Greenland, while others have documented increases in Hudson Strait (Hipfner et al. 2001, Falardeau et al. 2003).

Labrador has breeding populations of the northern common eider (*S. m. borealis*), the American common eider (*S. m. dresseri*) and intergrades of the 2 sub-species (Mendall 1986). Mendall (1980) documented this zone of overlap, but the geographic extent and consequences for population structure and recruitment have not been fully explored. Most information related to eider breeding ecology in Labrador is outdated (i.e., population trend) or unknown (i.e., migration routes and wintering locations). In terms of population affinities, eiders breeding in Labrador are thought to over winter in Atlantic Canada and the Northeastern United States (Palmer 1976, Goudie et al. 2000).

In 1998 the Canadian Wildlife Service (CWS) in conjunction with the Labrador Inuit Association (LIA), initiated surveys on the Labrador coast to collect information to estimate breeding eider population trends. These surveys were initiated in anticipation of the finalization of the LIA land claims, subsequent establishment of the Nunatsiavut land claim area and creation of natural resource co-management boards. Surveys covered approximately 750 km of the Labrador coast and were repeated annually from 1998 to 2003, but due to logistical reasons, not all islands were surveyed every year. I report the findings of these monitoring efforts and compare them with results from other studies.

STUDY AREA

I surveyed archipelagos near Nain and Hopedale from 1998-2003; St. Peter's Bay was surveyed in 1999, 2001, and 2002 (Chaffey 2003); and Rigolet was surveyed from 2000-2003. The Nain study area was approximately 2,237 km^2 and contained 811 islands ranging in size from 0.01 – 44,800 ha. The Hopedale study area was approximately 959 km^2 and contained 838 islands ranging in size from 0.01 – 3,875 ha. The Rigolet study area was approximately 3,172 km^2 and contained 348 islands ranging in size from 0.02 to 5,204 ha. The St. Peter's Bay study area was approximately 14 km^2 and contained 20 islands ranging in size from 0.03-23.43 ha.

All regions shared similar environmental characteristics such as a northern maritime climate, vegetation composed primarily of mosses, lichens, forbs, grasses, and sedges. The archipelagos of Nain, Hopedale, and Rigolet were typically comprised of barren islands with sparse vegetation and very limited nesting cover. Islands in St. Peter's Bay had more ground vegetation and woody cover, such as stunted black spruce (*Picea mariana*). All 4 archipelagos were classified as coastal barrens (Lopoukhine et al.

1978) and were considered to have a high-boreal ecoclimate (Meades 1990) and a low arctic oceanographic regime (Nettleship and Evans 1985).

METHODS

In all areas, I selected islands based on random or haphazard sampling (Chaulk et al. 2005). I limited my searches to islands that were estimated to be smaller than 30 ha. Since large islands require significant effort to search, I focused on smaller islands that could be easily censused by small field crews over restricted time periods. I conducted ground surveys using standard search methods employed by the Canadian Wildlife Service (Nettleship 1976) and other researchers (Falardeau et al. 2003, Merkel 2004); these consisted of 2 to 4 people systematically walking over the islands searching for signs of eider nesting. Islands in the 4 northern archipelagos had limited cover, and hens and unattended nests were easily detected. In several instances I stopped island searches because of weather or logistical considerations. If searches were halted, the island was classed as partially searched and was not used in trend analysis. I searched islands once per year. I initiated surveys in the south, and the survey crews moved north as the summer progressed; surveys were timed to occur during mid-incubation but actual timing varied slightly by archipelago and year (Table 4.1).

Sample sizes for the annual monitoring effort were estimated based on data collected in Nain and Hopedale during 1998 using the software program MONITOR and its exponential model (Users Manual, J.P Gibbs). I input island nest counts and an archipelago level standard deviation and varied the number of islands, surveys, and survey occasions to produce a matrix of possible sampling schemes that would generate statistical power > 0.80 with alpha = 0.10. Archipelago level standard deviation was

calculated using the bootstrap method (Sokal and Rohlf 1995). The sampling scheme matrix was used to guide sampling effort in post-1999 sampling years.

For trend estimation, I used nest counts from islands that were completely searched and ran the analysis using islands searched a minimum of 2, 3, and 4 years. Trends were estimated using the program ESTEQNINDEX, which fit the mean island nest count to a 2-way model with terms for year and island. Maximum likelihood estimates of year effects were calculated assuming observed counts had a Poisson distribution. An exponential trend was then fit through the year effects, and the jackknife estimate of the standard error was computed. This procedure was originally developed for analysis of the Breeding Bird Surveys and supports trend analysis with missing data (Collins 2003).

RESULTS

From 1998-2003, 117 islands (Table 4.2) were completely surveyed a total of 479 times in 4 archipelagos (Nain, Hopedale, Rigolet, St. Peter's Bay), and over this period I counted 13,185 eider nests. Average nest counts per island increased from a low of 3.3 in Hopedale in 1998 to over 10.7 nests/island in 2003, while in Nain average nest counts increased from a low of 14.5 in 1998 to over 46.3 in 2003 (Table 4.3). The most comprehensive study year was 2002, in which I sampled 109 islands in 4 archipelagos and counted 3,239 nests. These 109 islands represent about 5.8% of all islands on the Labrador coast < 30 ha.

Results based on islands surveyed a minimum of 4 years showed an average apparent annual increase of 21.6% for Nain, 13.4% for Hopedale, and 18.1% for all areas over the 6-year period from 1998-2003 (Table 4.4). These estimates varied slightly with

the number of survey years (e.g. the value for all islands surveyed a minimum of 2 years was 17.5% compared to 18.1% for islands surveyed a minimum of 4 years [Table 4.4]).

DISCUSSION

Due to logistics, not all islands were surveyed each year, and assessments based on archipelago level or year summaries tend to be misleading when plot or route data are missing. However the program ESTEQNINDEX allows for trend estimation with missing data (Collins 2003). Based on my analysis of average nest initiation dates, which ranged from a mean of 5 June in St. Peter's Bay to 23 June in Nain (Chaulk et al. 2004, Chaulk et al. 2005), I feel confident that my surveys were well timed to occur in mid to late incubation. On average about 71% of nests were classed as incubating, and only 10% were classed as hatched or hatching (Chaulk et al. 2005). Meanwhile, analysis of my sampling design suggests that within the subset of islands < 30 ha, the sampling effort was not spatially biased (K.G. Chaulk, Labrador Inuit Association, unpublished data). I feel confident that nest detection rates were high due to the absence of obscuring ground cover.

Recent studies of northern common eider population trends have shown drastic and disturbing patterns of population decline (Robertson and Gilchrist 1998, Suydam et al. 2000, Merkel 2004). In contrast my results show positive population growth for eider populations in Labrador. The average levels of population increase that I have detected are very high (13-22%). Given the geographic coverage of my surveys and the intensity of island searches that ranged from 2-4 archipelagos and 45-109 islands/year, I consider that my results are representative of common eider population trends in Labrador. From 1998 to 2003 average population growth in Nain was almost twice that of Hopedale.

Reasons for these regional differences are unknown but could be related to local environmental conditions and/or harvesting practices. However, I lack data for both these factors and can make no substantiated assessment at this time.

In 1980, Lock (1986) conducted aerial surveys for breeding eiders and estimated 15,000 pairs on the Labrador coast. During the mid-1990s the Canadian Wildlife Service conducted aerial surveys on the Labrador coast and estimated 30,000 breeding pairs of eiders and an annual growth rate of 3.7% per year during the intervening period (S. Gilliland, Canadian Wildlife Service, unpublished data). However these 2 surveys were not directly comparable given the different methodologies employed, so both the status and trend of eider populations remained unclear through the 1980s and 1990s. I am reluctant to use my data to generate population estimates, as my study was designed for trend estimation. Due to the limited quality of base maps, I have no way to determine what proportion of islands < 30 ha is actually suitable for nesting eiders. Some islands might be submerged at high tide, connected to mainland at low tide, offer little shelter from ocean storms, or have cabins situated on them. Previously I found that eider island occupancy ranged from 30-80% of islands surveyed, but these occupancy rates varied with archipelago (Chaulk et al. 2005). In the meantime, estimates of eider population size in Labrador will be unreliable until I can quantify the number of islands that are available and suitable for breeding.

Specific factors influencing eider population growth in Labrador could include improvement of environmental conditions or changes in migration patterns and subsequent changes in harvest on the breeding and wintering grounds. Other factors that may have influenced population growth include: nest shelter programs, eider

conservation-education programs, and reductions in eider bag limits during the 1980s and 1990s. In addition, the commercial Atlantic salmon (*Salmo salar*) and cod (*Gadus morhua*) fisheries were closed in the early 1990's. Researchers have identified human disturbance as a key factor influencing eider distributions and reproductive performance (Blumton et al. 1988, Johnson and Krohn 2002). Closure of these fisheries could have improved conditions for breeding eiders by reducing human disturbance near colonies (Chaffey 2003), reducing hunting on the breeding grounds, and eliminating by-catch in nets as a mortality source. In addition, large gull populations in Labrador appear to be declining (Robertson et al. 2002) and may have further improved breeding conditions for eiders through a reduction in avian predation rates.

Based on the information presented above, I think there are numerous reasons why breeding eider populations in Labrador are increasing. However I am not certain why an adjacent population in southwestern Greenland is declining (Merkel 2004). It has been suggested that hunting is the main factor causing the decline in Greenland, where eiders are subjected to unsustainable harvest (Merkel 2004). Meanwhile, no recoveries of eiders banded in Labrador have been reported in Greenland (Lyngs 2003), suggesting little or no connection between the 2 populations. Researchers have suggested that Labrador eiders winter in Newfoundland, Quebec, and the Maritimes (Palmer 1976, Reed and Erskine 1986, Wendt and Silieff 1986, Goudie et al. 2000) and may experience lower harvest levels than eiders that winter in Greenland.

Typically eiders have deferred sexual maturity and exhibit low rates of annual recruitment, and reproduction (Coulson 1984) and population growth is tied to adult survival (Goudie et al. 2000). However, eider populations can apparently sustain dramatic

rates of increase, especially during population re-growth. Chapdelaine (1995) documented 11.3% and 23.5% annual growth for common eiders breeding in the Gulf of St. Lawrence. While a number of eider populations in the Netherlands grew at rates between 17-28%, this occurred during the early stages of colony growth, and was credited to low mortality, and high rates of recruitment (Swennen 2002). Meanwhile, 25-35% per year increases were observed at newly established Danish colonies due mainly to immigration (Bregnalle et al. 2002).

The extent that anthropogenic factors influenced overall eider population dynamics in Labrador in the 20th century is unknown, yet my evidence suggests significant population increases during the late 1990's and early 21st century. These growth patterns are similar to those recently observed in Newfoundland (S. Gilliland, Canadian Wildlife Service, personal communication) and the Gulf of St. Lawrence (Chapedelaine 1995), and is a promising trend for a species undergoing declines throughout much of its range.

CONCLUSION

If general conditions remain constant, I feel that current eider harvest levels in Labrador are sustainable, at least in the short-term. Given the baseline information that is now in place I recommend continued population monitoring on a 3 to 4 year rotation. I also suggest expanding study scope to include un-surveyed portions of the Labrador coast. A rigorous assessment of suitable breeding islands is also suggested, and once complete, I recommend that regional population estimates be generated.

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Table 4.1. Survey dates by year and archipelago for nesting common eiders on the coast of Labrador from 1998-2003.

Year	Nain	Hopedale	Rigolet	STP
1998	6 - 10 July	30 June - 4 July		
1999	13 - 15 July	4 July - 12 July		22-23 June
2000	3 - 9 July	28 - 30 June	20 - 26 June	
2001	5 - 19 July	4 - 17 July	18 - 27 June	11 June
2002	13 - 22 July	3 - 17 July	17 - 22 June	5-9 June
2003	11 - 13 July	3 - 7 July	14 - 20 June	

+ STP is an abbreviation for St. Peter's Bay

Table 4.2. Sampling effort from 1998-2003 and summary of islands and their sizes for each archipelago surveyed on the Labrador coast from 1998-2003.

Archipelago	Number of islands < 30 ha searched between 1998-2003	Number of islands in archipelago	Number of islands < 30 ha in archipelago	% searched	
				Total	< 30 ha
Nain	36	811	740	4.4	4.9
Hopedale	49	838	789	5.8	6.2
Rigolet	22	348	326	6.3	6.7
STP+	10	20	20	50.0	50.0
Total	117	1995	1875	5.9	6.2

+ STP is an abbreviation for St. Peter's Bay

Table 4.3. Average ± SD number of nests per island by archipelago and year[1]. Data collected on the Labrador coast from 1998-2003.

Archipelago	1998	1999	2000	2001	2002	2003
Nain	14.5 ±19.6	17.6 ±23.9	21.6 ±26.3	32.4 ±24.1	40.7 ±52.4	46.3 ±51.9
Hopedale	3.3 ±7.1	4.3 ±7.8	5.7 ±9.8	4.8 ±7.7	5.4 ±8.4	10.7 ±20.4
Rigolet			90.5 ±153.9	144.9 ±195.9	74.9 ±86.9	141.3 ±167.1
STP+		55.9 ±57.0		81.0 ±93.0	42.9 ±51.1	

[1] Note that these average values do not take into account missing data (some islands were not searched every year) and are presented as general information.

+ STP is an abbreviation for St. Peter's Bay

Table 4.4. Apparent annual change (%) in breeding common eider populations on the Labrador coast from 1998-2003. Due to limited samples sizes values for Rigolet and St. Peter's Bay were not presented individually (see footnote). These values are based on an analysis conducted using the program ESTEQNINDEX, which calculates population trend with missing data (Collins 2003).

Archipelago	Minimum Number of Survey Years	Number of Islands used in the Model	Apparent Annual Percentage Change in Breeding Population	95 % CI Lower	Upper
Nain	4	21	21.6	1.6	35.8
	3	26	21.6	6.1	39.5
	2	36	22.4	7.5	39.2
Hopedale	4	34	13.4	2.4	25.6
	3	40	13.1	2.2	25.3
	2	49	14.8	3.8	26.8
All	4 [a]	58	18.1	6.7	30.7
	3 [b]	79	17.5	6.7	29.4
	2 [b]	117	17.5	8.2	27.5

[a] includes Islands from Nain, Hopedale & Rigolet [b] includes islands from Nain, Hopedale, Rigolet & St. Peter's Bay.

CHAPTER TRANSITION

In this chapter I use modern population analysis techniques, and found that eider populations on the Labrador coast were apparently increasing from 1998-2003, although there was much regional and annual variation in the trends. This information is certainly important for management purposes but also has utility for interpreting other findings of this thesis in a larger theoretical context. Many predictions about relationships between population distribution and abundance are based on stable populations; but patterns may be different in growing populations. Therefore, understanding population growth is an important step in evaluating both abundance and distribution. In the next Chapter in an attempt to determine factors that influence eider nesting distributions and to address the question of why eiders nest where they nest, I investigate the relationship between landscape features, intertidal resources and nesting eider distribution and abundance.

DO ABIOTIC LANDSCAPE FEATURES INFLUENCE ABUNDANCE, INCIDENCE, AND DISPERSION IN A COLONIAL MARINE BIRD?

ABSTRACT: Factors that influence individual and colony spacing are still not well understood in many organisms. Common eiders (*Somateria mollissima*) are colonial seaducks that nest on coastal islands and forage in intertidal and shallow subtidal waters. I assessed the associations between eider nest abundance and amount of foraging area (shoreline) and intertidal prey density. Unexpectedly, nest abundance was not related to intertidal prey abundance or the amount of shoreline (foraging area) in a given area. At the 104 km^2 scale, intertidal shoreline length was positively related to the number of islands, but eider nest abundance, incidence, and the coefficient of dispersion were all negatively related to the number of islands and the amount of island shoreline. Also at the 104 km^2, the extent of spring ice cover was positively related to the number of islands but ice cover was negatively related to eider nest abundance, and the coefficient of dispersion. However there were scaling effects with most relationships becoming weaker at a larger (455 km^2) spatial scale, except for ice cover and abundance and ice cover and the coefficient of dispersion which were significant at both spatial scales. I suggest that eiders are facultative colonial nesters and that areas with many islands will trap ice. The ice in turn, forms bridges that provide access to nesting islands by terrestrial predators. At the 104 km^2 grid scale, there was a positive relationship between eider incidence (occupancy of islands) and abundance; at higher colony sizes, more local islands tended to be occupied. My findings show that eiders respond to landscape features that influence spatial connectivity via ice cover; a feature that will be influenced by climate change.

Many mechanisms influence the distribution of colonial species (Krebs and Davies 1987, Anderson and Titman 1992). Foraging opportunities, predator avoidance, increased vigilance, brood amalgamation, and mating opportunities have all been cited as possible benefits of group living (Powell 1974, Munro and Bédard 1977, Bertram 1978). However, there are many costs associated with group living including: disease transmission, brood parasitism, competition for mates and other resources, increased conspicuousness, and prey depletion (Ashmole 1963, Alexander 1974, Furness and Birkhead 1984, Cairns 1989).

Food availability is often seen as one of the most important factors influencing the distribution and size of bird colonies (Ainley et al 2003). Furness and Birkhead (1984) and Cairns (1989) demonstrated that some colonies were geographically dispersed and suggested that food availability and competition were primary factors influencing colony spacing; both are logical explanations for central place foraging species that rear and feed their young in the nest. However for species that do not feed during incubation or feed chicks at the nest site, proximity to resources may be less important when selecting nesting sites.

Common eider (*Somateria mollissima*) females do not feed during incubation (Milne 1976, Korschgen 1977, Parker and Holms 1990, Erikstad and Tveraa 1995) and are known to experience extreme weight loss during the incubation period (Korschgen 1977). Christensen (2000) argued that the final critical phases of eider egg formation occur just prior to laying, if sufficient energy is not consumed during the pre-laying

period, female energy reserves may be insufficient for clutch formation and nest attention during incubation. However the demonstrated importance of food resources and habitat quality for eiders as a determinant in the selection of breeding islands remains uncertain (Christensen 2000). Schmutz et al. (1983) reported that food near breeding islands in Hudson Bay was unimportant, while in Europe it has been reported that the availability and quality of food near eider breeding islands can have a significant impact on breeding success (Oosterhuis and van Dijk 2002). Furthermore, because common eiders prefer to forage is shallow sub-tidal waters (Larsen and Guillemette 2000), the amount of shoreline in a given area could provide a proxy of suitable foraging habitat.

Some researchers have suggested that predators strongly influence eider nesting behaviour (Quinlan and Lehnhausen 1982, Robertson 1995, Bolduc and Guillemette 2003), e.g. fasting by incubating eiders is considered to have evolved as an anti-predator strategy (Swennen 1983, 1989; Gotmark 1989; Erikstad and Tveraa 1995). Mammalian predators usually have the most negative effect on nesting eiders, often resulting in the decimation of all clutches on a given island (Goudie et al 2000).

With respect to landscape, Huffaker (1958) suggested that spatial heterogeneity tended to increase population stability. This notion has been supported by many other researchers as well (May 1978, Sabelis and Diekmann 1988, Hassell et al 1991, Murdoch 1994). That is, populations in complex spatial environments persist in the presence of localized negative impacts (i.e. predators, disease) better than population in continuous space. The reason is that discontinuous space itself will act as a barrier to the spread of the negative impacts (i.e. predators). Therefore I hypothesized that landscape continuity and heterogeneity might influence the size and distribution of eider colonies.

In the context of nesting islands in northern areas, ice cover in spring can reduce spatial heterogeneity by increasing connectivity among islands for terrestrial predators (Parker and Mehlum 1991). Many researchers have suggested that eiders often wait to nest until ice bridges between islands and mainland have melted (Lack 1933, Ahen and Andersson 1970, Quinlan and Lehnhausen 1982). Ice cover may also negatively influence habitat suitability by reducing access to near shore foraging habitat, although Guillemette et al (1993) reported that during winter foraging eiders have a high threshold for ice obstruction. Parker and Mehlum (1991) found that in years with late spring ice break-up, the number of available nesting islands was limited, which lead to higher nesting densities at ice free colonies. Therefore it is possible that spring ice cover could influence colony size and distribution of nesting common eiders.

I use inter-tidal sampling to examine relationships between common eider distribution and abundance patterns with intertidal prey abundance. I used geographic analysis to test relationships between common eider distribution and abundance and landscape features, including ice cover. Specifically, I investigated relationships between eider abundance and prey, and relationships between the number of islands, amount of shoreline, ice cover, with eider abundance, incidence, and dispersion. Possible explanations for observed patterns are discussed.

METHODS

Archipelagos near the communities of Nain, Hopedale and Rigolet in northern Labrador were surveyed for nesting common eiders between 2000 and 2003 (Figure 5.1). All regions shared similar environmental characteristics including a northern maritime climate. All three archipelagos are classified as coastal barrens (Lopoukhine et al. 1978)

and are considered to have a high-boreal ecoclimate (Meades 1990) in a Low Arctic oceanographic regime (Nettleship and Evans 1985). Islands in this region were typically barren with sparse vegetation composed primarily of mosses, lichens, forbs, and grasses, providing very limited nesting cover, so both hens and unattended nests were easily detected. In all areas, islands were selected for study based on random sampling. Because eiders in Labrador typically nest on small barren islands (Chaulk et al. 2004), I limited my searches to islands that were smaller than 30 ha. Ground censuses were conducted using standard search method employed by the Canadian Wildlife Service (Nettleship 1976, Chaulk et al. 2004).

Intertidal Sampling

In 2003, I randomly selected a subset of previously surveyed islands, consisting of 27 islands in the three archipelagos. At these islands I sampled intertidal habitat and censused nesting eiders. Intertidal sampling was conducted between low and mid-tide only, direction of movement around the island was chosen randomly by a coin toss. Four to six rectangular quadrats (1280 cm^2 each) were sampled at each island (in rare cases sampling was halted because of weather conditions, or rising tide). The purpose of this sampling was to assess broad scale relationships between intertidal prey abundance and eider nest abundance.

All organism types in each quadrat were identified to species using field guides (Kavanagh and Leung 2001, Gosner 1978) where possible; if not, organisms were identified to genus or family. Percent ground cover per quadrat was estimated for each species. Because of the 3 dimensional nature of the sampling areas, rarely total combined ground cover of all species exceeded 100%. Throughout my analyses I use average

ground cover of intertidal species/island to compensate for unequal sampling effort, as the actual number of sampled quadrats per island varied from four to six.

In some cases, variables were log transformed to normalize their distributions. I used a general linear model (GLM) to test common eider nesting abundance (log) against the abundance (log) of three intertidal species (mussel, periwinkle, knotted wrack) that are important food sources for eiders and their young (Guillemette et al 1992; Goudie et al. 2000; Hamilton 2000, 2001). My hypothesis was that eider nest abundance would be highest in areas with highest densities of prey (mussel, periwinkle) and/or important habitat (knotted wrack).

Coastal Landscape

To examine relationships with landscape features, I used common eider nesting census data collected in 2002, my most intensive sampling year. Two rectangular grid system were created, one grid was comprised of numerous 104-km^2 cells, the second grid system was comprised of numerous 455 km^2 cells. The grid systems were created using a spherical projection system and superimposed on the surveyed islands in a geographic information system (Mapinfo 7.5). Structured query language was used to reduce the grid network to cells containing surveyed islands. Cells containing fewer than 3 censused islands were not used in the analysis. Mean eider abundance was calculated based on censused islands within each grid cell, while the landscape features (number of islands, and total shoreline) were based on all islands located within each grid cell.

The size of the grid cells were determined based on the following criteria, they had to be large enough to include a) at least 3 surveyed islands per grid cell and this determined the minimum size of the smaller grid network b) at least 12 grid cells per

network, and this determined the maximum size for the larger network. The 3 islands per grid cell were to ensure the statistical minimum to calculate both the average and variance for incidence and abundance per grid cell. The 12 grid cell minimum per network was to ensure sufficient sample size for grid cell analysis. These two parameters set the limits for size of the grid systems and tended to work against each other.

Thus the lower limit for the smaller grid system was determined to be approximately 90 km2 per grid cell. Using grid cells smaller than 90 km2 would mean that most grid cells would contain less than 3 sampled islands. In the end the size of the grid cells of the smallest grid network was 10 km by 10 km, which is a simple rounded number that met the sampling basic criteria. But the 10 by 10 km grid system was created on a Euclidean surface, (i.e., a non projected computer matrix). When the grids were imported into a GIS they were distorted by the earth's imperfect curvature (which is non-euclidean), and by projection distortions which are common in mapping. This meant the grid cells were slightly distorted from original size, the end result was the grid cells were about 104 km2 give or take 0.5 of a km2.

The larger grid system had the same basic criteria, accept that with the larger system the limiting factor was ensuring enough grid cells for analysis (N = 12). The threshold here was estimated to be 25 by 25 km or 625 km2 per grid cell. For example if the grid system was composed of one grid cell measuring 1000 km by 1000 km, it would have encompassed the entire study area, but N = 1. In the end the maximum size of the larger grid network was rounded to 20 km by 20 km, or 4 times the size of the smaller grid network. However with the mapping distortions mentioned above the grid cells ended up being closer to 455 km2.

I used the simplest and most widely used method to assess colony size distribution: the variance to mean ratio or the coefficient of dispersion (Taylor 1961). The coefficient of dispersion was calculated by dividing total variance of nest count per grid cell by mean abundance per grid cell. When the coefficient of dispersion (CD) = 1, distribution is random; when CD < 1 distribution is uniform; when CD is > 1, distribution is aggregated. I also ran a binary logistic regression model to test the relationship between the presence of nesting common eiders on islands (incidence) and the number of islands in a grid cell.

Ice Cover

A satellite photo (8 June 2002, Figure 5.2) of the study area was downloaded in raster format and geo-referenced in MapInfo (image source: NASA/Visible Earth). This photos was selected because of geographic coverage and because the image date coincided well with the study and general eider nest initiation dates in northern Labrador (12 June ± 12 d, range = 21 May to 9 July; Chaulk et al. (2004). Ice cover was estimated at two grid scales (104 km^2 and 455 km^2).

Grid systems were superimposed on the satellite image. For comparisons between ice cover and eider distribution and abundance only grid cells containing 3 or more surveyed islands were used. Percent ice cover was estimated for each grid cell, and was then converted to total ice cover per grid cell in hectares (ha). I then tested whether ice cover was related to common eider abundance, incidence, and coefficient of dispersion. My *a priori* hypothesis was that ice cover would be positively related to the number of islands within a given area, and that eider abundance, incidence and dispersion would be negatively related to number of islands and ice cover.

Statistics

I used Minitab 14 (Minitab Inc. 2003) for all statistical testing and graphing. For binary logistic regression models, I present *P*-values for Hosmer-Lemeshow goodness of fit statistic, which assesses the fit of the logistic model against actual outcomes. The Hosmer-Lemeshow goodness of fit statistic is a form of a Pearson chi-square statistic, and $P > 0.05$ suggest that the model fit the data well (Peng et al. 2002). Residuals were checked for all models, and all tests were two tailed with critical alpha set to 0.05; all +/- values are standard errors.

RESULTS

Sampling effort and geographic coverage varied by study component (Table 5.1). In 2003, I sampled 163 quadrats on 27 islands, and identified 19 species, 9 of which were found on 2 or less islands (Table 5.2). Interestingly, the general linear model revealed that neither mussel, periwinkle or knotted wrack had a significant relationship with eider abundance (Coefficient $_{mussel} = -0.05 \pm 0.64$, $P_{mussel} = 0.94$, Coefficient $_{periwinkle} = 0.06 \pm 0.09$, $P_{periwinkle} = 0.50$, Coefficient $_{knotted\ wrack} = 0.30 \pm 0.22$, $P_{knotted\ wrack} = 0.2$, df =26, $R^2 = 28.0\%$). I used the GLM to assess possible relationships with other inter-tidal species but no significant relationships were found.

Landscape (104 km^2 scale)

In 2002, I sampled 89 islands within 18 grid cells at the ~104 km^2 scale (Table 5.1). Not surprisingly, the length of shoreline and the number of islands in each grid cell were positively related (Table 5.3, Figure 5.3). To simplify the data presentation I report tests based on the number of islands, but note that relationships with shoreline length were similar. Interestingly, I found a significant negative relationship between mean eider

abundance and number of islands within a grid cell (Table 5.3, Figure 5.3). There was also a significant negative relationship between incidence and number of islands (Table 5.3, Figure 5.3). I also found a significant negative relationship between the coefficient of dispersion and number of islands, with dispersion approaching unity (CD = 1) at the highest island densities (Table 5.3, Figure 5.3).

Also at the 104 km^2 scale, ice cover was positively related to the number of islands in a grid cell (Table 5.3, Figure 5.3). I also found a significant negative relationship between mean eider abundance and ice cover in a grid cell (Table 5.3, Figure 5.3). Interestingly, the relationship between eider incidence and ice cover in a grid cell was not statistically significant (Table 5.3, Figure 5.3). There was a significant negative relationship between the coefficient of dispersion and ice cover in a grid cell (Table 5.3, Figure 5.3). When evaluated without reference to landscape features, I found a significant positive intraspecific relationship between eider incidence and abundance (Table 5.3, Figure 5.3), indicating that at higher eider nesting abundance, more islands were occupied.

Scale Effect

Using data from 2002 but at the 455 km^2 scale, I ran the same analyses listed above. At the 455 km^2 scale, I only found two tests to be significant. Ice cover was a significant negative predictor of mean abundance, and ice cover was a negative predictor of the coefficient of dispersion (Table 5.3, Figure 5.4). These findings suggest a scaling effect with islands playing a more important role at smaller spatial scales, and ice cover being important across spatial scales.

DISCUSSION

It has been long recognized that physical landscape features influence animal and plant distributions (Wallace 1878). Yet there are few investigations of the role of the physical landscape with respect to the distribution and abundance of bird colonies. Findings from other bird species suggest geographic dispersion of colonies is not always the case (Ainley et al. 1995), but when colonies are dispersed these patterns are often explained by interactions with local food resources (Furness and Birkhead 1984, Cairns 1989), or site limitations (Kaiser and Forbes 1992).

Intertidal prey

Throughout the sub-arctic, common eiders generally prefer to feed on blue mussel, but females and young often feed extensively on amphipods and periwinkles (Hamilton 2001, Goudie et al 2000). Hamilton (2001) found that knotted wrack was an important habitat feature for young eiders and attributed this relationship to increased prey abundance. As such, I hypothesized that if eider nesting abundance was influenced by food, it would be highest in areas with greatest abundance of mussels, periwinkles and/or habitats with knotted wrack.

It appeared that eider abundance on nesting islands was not related to intertidal prey abundance. One explanation may be that during pre-nesting period eiders over-graze intertidal invertebrates around a given island, a form of prey depletion (Ashmole 1963, Birt et al. 1987). Alternatively, common eiders may not select breeding islands based on the local food supply. For example, pre-flight ducklings are known to follow hens to foraging areas that are located over 80 km from the nest (Cooch 1965). Post-hatch dispersal behaviour may enable eiders to select nest sites on features than other

proximity to food. Finally ice may scour the intertidal area removing most of the intertidal prey items preferred by nesting eiders.

Landscape and Foraging Habitat

A positive relationship between eider abundance and waterdepth has been previously suggested (Guillemette et al. 1993), because deep water reduces eider foraging efficiency (Ydenberg and Guillemette 1991, Guillemette et al. 1993, MacCharles 1997). Common eiders are generalist feeders and typically feed at depths < 10 m (Goudie et al 2000, Larsen and Guillemette 2000) and much less than that for young eiders (Hamilton 2001). One of the main foods of the common eider is the blue mussel (Cottam 1939, Goudie et al. 2000, Larsen and Guillemette 2000), which is mainly found in shallow sublittoral waters (Newell 1989).

Given these factors, positive relationships between shoreline length, shallow foraging habitat, and eider abundance might be predicted. In fact my data, at the scale of tens of square kilometers, suggest the opposite, in that abundance and incidence are negatively related to the amount of shoreline. These findings suggest that general landscape features, which are thought to be related to foraging habitat, may be related to colony size, but not in the expected way. It should also be noted that water depth and subsurface contouring (bathymetry) likely influence foraging suitability. However, because of the limited quality and coverage of hydrographic charts for this remote region, I was not able to investigate the role of bathymetry as an abiotic landscape feature.

Landscape and Ice

In general, I found that the number of islands and ice cover in a given area were negatively related to eider abundance, incidence and dispersion. Of these two predictors,

ice cover was important at both spatial scales, while the number of islands only seems to be important at smaller spatial scales. To explain why abundance and incidence are negatively related to island density and ice cover, I suggest two general explanations. First, I suggest that eiders are facultative colonial nesters, and as more islands are available nesting females disperse, consistent with an ideal free distribution (Fretwell and Lucas 1970), or source sink population dynamics (Pulliam 1988). In addition, as numbers of islands increase so to does the tendency for an archipelago to trap ice. Increased ice in turn could reduce the overall attractiveness of an archipelago to nesting eiders, because ice bridges between islands and the mainland, provide mammalian predators access to the nesting sites.

In Finland, higher eider nest densities were found to be positively related to island isolation which in turn was related to reduced predation and earlier ice break up (Laurila 1989). Parker and Mehlum (1991) reported that late break-up of sea ice limited the number of islands available for nesting, while Robertson (1995) found that nests on islands farther from the mainland were less likely to be depredated by arctic foxes. Northern predators such as arctic foxes and polar bears (*Ursus maritimus*) are adapted to winter conditions and are attracted to pack ice (Banfield 1974). Johnson and Krohn (2002) investigated numerous habitat characteristics for nesting common eiders, including cover and distance to other islands. Eider presence was positively correlated with increasing distance from islands greater than 50 ha, and with nest cover. The former suggests that nearby landscape features can influence colony distribution and the later that cover from predators is important.

Increased ice could also mean colder conditions and/or reduced access to food resources. For example, heavy ice during winter is known to lead to starvation in eiders (Barry 1986, Fournier and Hines 1994) and has been suggested as a cause of population decline (Robertson and Gilchrist 1998). Similar processes could occur in response to heavy ice during the early nesting phases and could affect colony distributions. Unfortunately my study could not differentiate whether predation, colder conditions and/or reduced access to food were causing these patterns; in fact all of these factors could play interactive roles. Regardless, landscape features, as they relate to the dynamics of spring ice break-up, appear to influence the abundance and dispersion of nesting common eiders. These processes are directly linked to early spatial models (Huffaker 1958) that demonstrated landscape heterogeneity can increase population stability. They are also highly relevant to considerations of climate change and ocean ice conditions (Stirling et al. 2004).

It should be noted that the behaviour of pack ice (trapped or deflected) relative to archipelago structure is likely to be influenced by many interacting factors such as wind, ice pan size, inter-island distance, tides and ocean currents. Therefore heavy pack ice might not be expected in dense archipelagos every year. Seasonably predictable environments are important for many northern species that show high survival, low fecundity life history strategies, thus alternating annual patterns of pack ice could also change the attractiveness of a given archipelago to breeding eiders. This would lead to different nesting distributions across years or other nesting parameters such as clutch size and laying dates (Chaulk et al. 2004), and would reduce natal and breeding philopatry to specific islands in some areas (Parker and Mehlum 1991, Bustnes and Erikstad 1993).

These interactions are likely to be further complicated by the common eiders' tenacity to specific nest sites (Cooch 1965, Parker and Mehlum 1991). Consequently over long time scales I would predict the highest nesting densities in archipelagos with the least variance in ice cover/open water during the spring period.

Dispersion

The coefficient of dispersion was negatively related to the number of islands, meaning that at high island numbers common eiders were distributed randomly across islands, but when island numbers were low nesting eiders were highly aggregated. These patterns are expected if colonial behaviour serves to: reduce individual predation risk (Schmutz et al. 1983), mirror the distribution of food resources or because the number of islands themselves directly influence distribution patterns (Kaiser and Forbes1992).

With respect to predation, terrestrial predators are likely to be of greater risk in high island density archipelagos, because of increased connectivity, while at low island densities, avian predators, such as gulls, may be a greater threat and aggregated nesting may deter gulls from depredating nests (e.g. Kruuk 1964, Götmark and Åhlund 1984, Swennen 1989). Such relationships are consistent with findings in Norway, where coloniality was found to be facultative, in that when more islands were available eider distribution increased, decreasing nest densities (Parker and Mehlum 1991).

My results have implications for the management of other gregarious organisms, especially in regions where habitat availability is low, and colony size or population density are high. A key result is that habitat availability may not be a simple function of amount of habitat. Instead availability may be mediated by spatial connectivity, especially in systems that are regularly influenced by predators, disease, and seasonal events such as

fire or ice. Interestingly, in some southern portions of the eider's range spring ice may play a less important role and this may explain why southern colonies tend to be very large, since the occurrence of ice, and terrestrial predation are less severe, although the limited availability of nesting islands likely also plays a role in these regional differences (Brown and Bomberger Brown 2001).

Incidence and Abundance

Across all landscape features, at the scale of 104 km^2 I found that eider abundance and incidence were positively related. In other words, when colony sizes were larger, common eiders occupied more islands, consistent with patterns predicted under the ideal free distribution (Fretwell and Lucas 1970), source sink population dynamics (Pulliam 1988), or metapopulation processes (Levins 1969, Hanski 1999). I interpret this to imply a sort of rescue effect, whereby in high density areas, more local patches are occupied due to overflow from the highest density patches (Hanski 1999).

Using population simulations, Venier and Fahrig (1996) found that intra-specific incidence and abundance was positively related to habitat availability. This is interesting since I also found a positive relationship between incidence and abundance, but this relationship was maintained through simultaneous negative relationships with habitat availability (i.e. number of islands). I suggest that habitat quality decreases with island density because of bridging effects by ice and increased access by predators.

Overall my findings suggest that landscape features can be a determinant of marine bird distributions, but the relationship may not be as simple as expected, especially in high latitude regions where ice may play an important role. Studies

involving sea ice influences on animal distributions will of particular value in assessing the biological consequences of climate variability and change.

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Table 5.1. Summary of sampling effort and major landscape features by study component for 2002-2003 on the north Labrador coast (± = 1 SE).

	Intertidal	Landscape	Ice
Year	2003	2002	2002
Average number of Islands		75 ± 36	62 ± 7.96
Average Island area (ha)		1548 ± 1678	3127 ± 626
Average Mainland area (ha)		100121 ± 5102	16484 ± 1489
Average Ice cover			41669 ± 723
Size of Grid Cell	1280 cm^2	104 km^2	455 km^2
Total Quadrats or Grid Cells	163	18	88
Total Islands surveyed for Eiders	27	89	79
Total Islands in grid system		1349	5472

Table 5.2. Estimated ground cover of inter-tidal species found on 3 or more islands on the Labrador coast in 2003.

Scientific Name	Common & Local Names	Mean (cm^2) ± 1 SE	Total all Samples (cm^2)
Lunatia heros	Northern moon snail	8.5 ± 2.2	245.3
Desmarestia spp.	Sourweed	15.5 ± 9.9	448.0
Orchestiidae	Beach flea	18.9 ± 5.9	547.0
Unknown	Unknown green algae	54.1 ± 22.2	1569.1
Littorina spp.	Periwinkle	67.0 ± 34.6	1943.9
Mytilis edulis	Blue mussel	67.9 ± 27.6	1969.1
Unknown	Unknown brown algae	93.8 ± 49.7	2720.0
Ascophyllum nodosum	Knotted wrack	128.1 ± 50.9	3716.3
Balanus spp.	Barnacles	142.8 ± 33.7	4142.1
Fucus spp.	Rockweed	598.6 ± 57.9	17358.1

Table 5.3. Summary of statistical tests, organized by spatial scale, predictor and response. For general linear models were report F scores, and R^2 values, for binary logistic regression models I report Z scores, and the Hosmer-Lemeshow (HL) goodness of fit statistic. For all models I present the regression coefficient (± 1 SE), the degrees of freedom, and the P value of the test.

Scale	Predictor	Response	Coefficient (± 1 SE)	F	Z	DF	P	R^2	HL
104 km^2									
	Islands	Shore	0.96 ± 0.16	33.9		17	0.000	68.00	
	Islands	Abundance	-0.47 ± 0.16	8.5		17	0.010	34.80	
	Islands	Incidence	-0.026 ± 0.007		-3.2	1	0.001		0.61
	Islands	Dispersion	-0.38 ± 0.13	8.0		17	0.010	33.30	
	Islands	Ice	75.81 ± 25.71	8.7		17	0.009	35.20	
	Ice	Abundance	-0.004 ± 0.001	15.6		17	0.001	49.40	
	Ice	Incidence	-0.0002 ± 0.0001		-1.9	1	0.055		0.11
	Ice	Dispersion	-0.004 ± 0.001	43.0		17	0.000	72.90	
	Abundance	Incidence	2.01 ± 0.62		3.2	1	0.019		0.88
455 km^2									
	Islands	Shore	0.596 ± 0.327	3.3		7	0.119	35.00	
	Islands	Abundance	-0.06 ± 0.22	0.1		7	0.809	1.00	
	Islands	Incidence	0.0007 ± 0.0019		0.4	1	0.698		0.31
	Islands	Dispersion	0.02 ± 0.53	0.0		7	0.973	0.02	
	Islands	Ice	-4.12 ± 14.87	0.1		10	0.788	0.80	
	Ice	Abundance	-0.023 ± 0.006	13.4		7	0.011	69.07	
	Ice	Incidence	-0.0001± 0.0001		-0.9	1	0.359		0.22
	Ice	Dispersion	-0.06 ± 0.01	28.5		7	0.002	82.60	
	Abundance	Incidence	0.0085 ± 0.0070		1.2	1	0.226		0.11

Figure 5.1. Study area in northern Labrador.

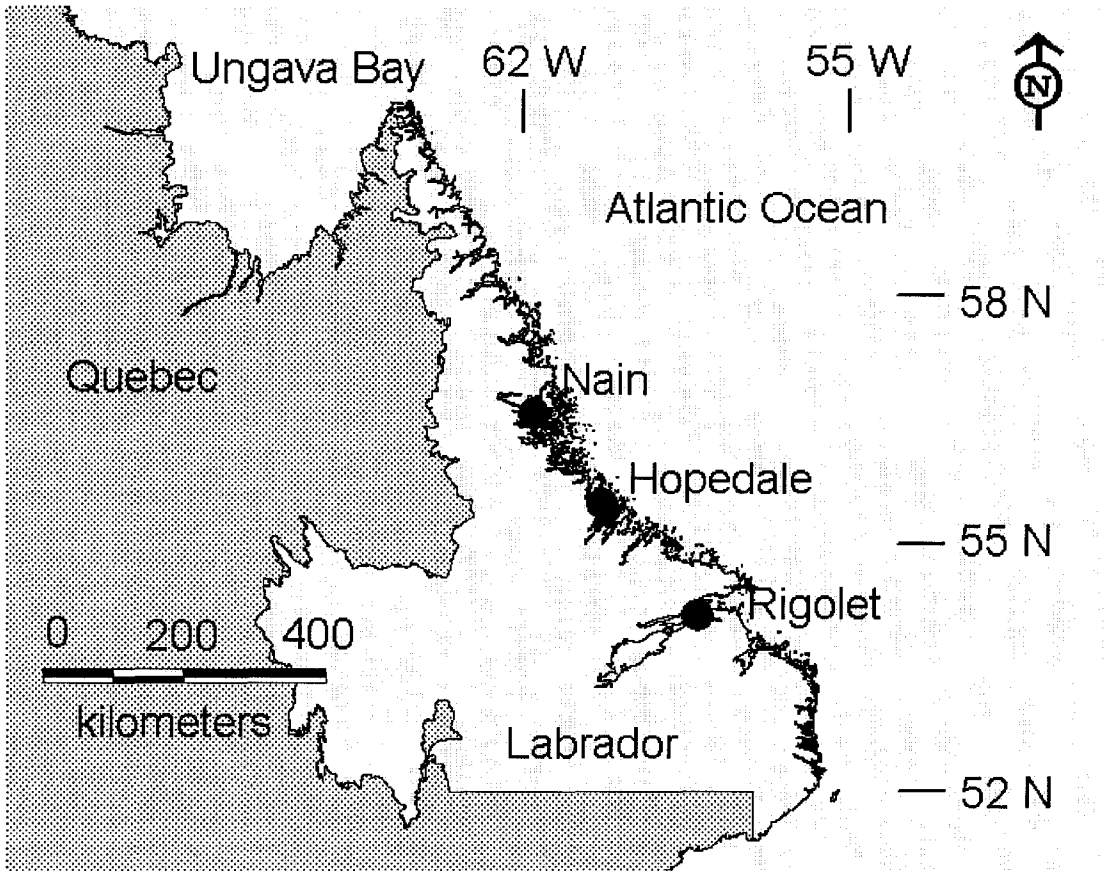


Figure 5.2. Satellite image of the Labrador coast taken on 8 June 2002 (source: NASA/Visible Earth).

Figure 5.3. Relationships among landscape features, ice cover and eider nesting abundance and distribution. All data are based on 18 grid cells at the 104 km^2 scale and nesting surveys were conducted on the Labrador coast in 2002.. In plots including the coefficient of dispersion, dashed horizontal line indicates a coefficient of dispersion (CD) = 1, where the population is randomly dispersed.

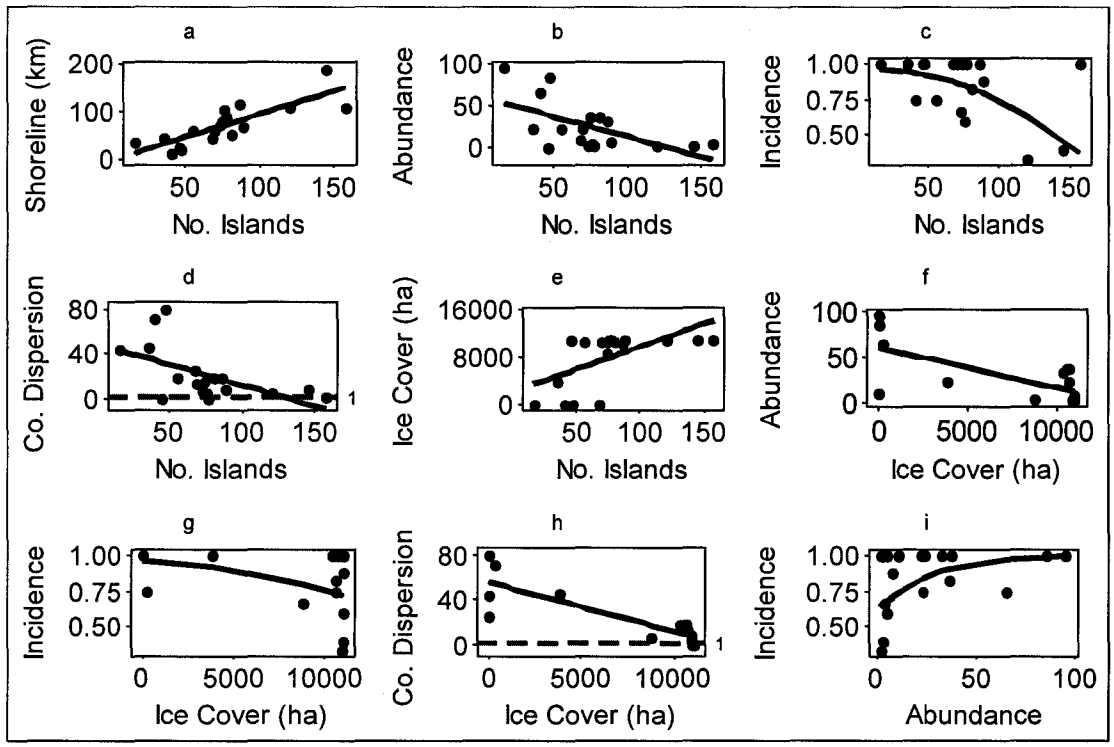
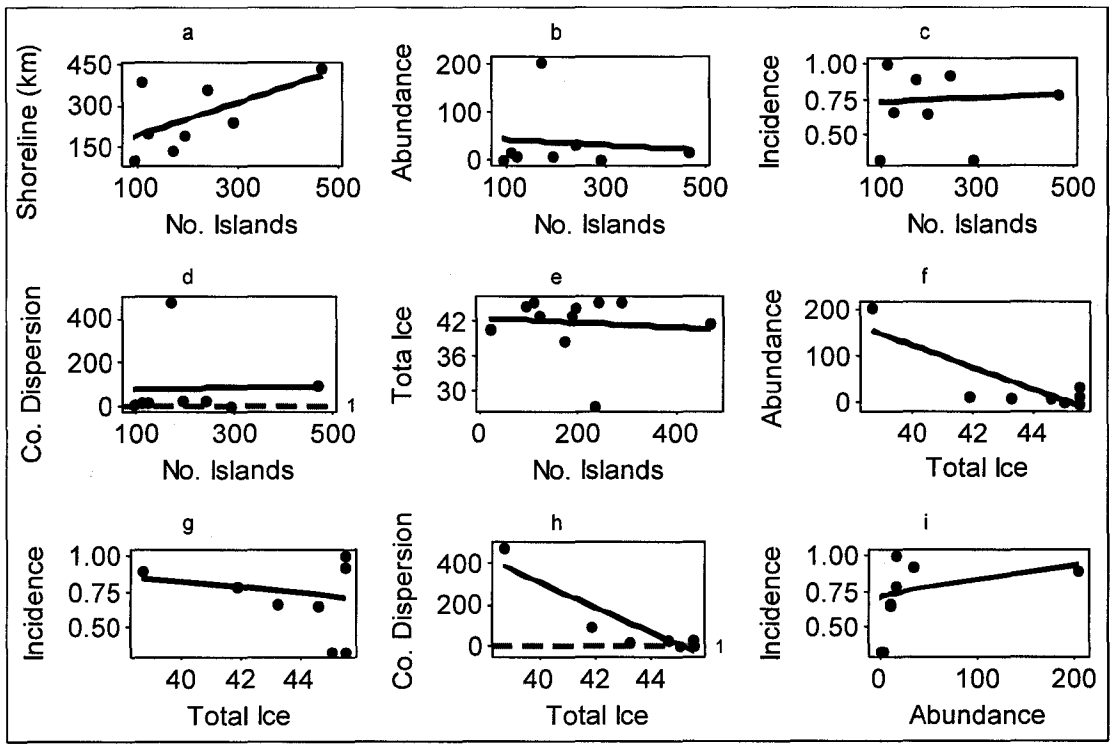


Figure 5.4. Relationships among landscape features, ice cover and eider nesting abundance and distribution. All data are based on 11 grid cells at the 455 km^2 scale and nesting surveys were conducted on the Labrador coast in 2002.. In plots including the coefficient of dispersion, dashed horizontal line indicates a coefficient of dispersion (CD) = 1, where the population is randomly dispersed. Also note that total ice is in 1000's of hectares.



CHAPTER TRANSITION

In this Chapter I found that landscape features and ice cover were important factors influencing eider nesting distribution and abundance along the Labrador coast, while no relationships were between intertidal resources and eider nesting distribution and abundance. From this Chapter I conclude that abiotic features, namely ice cover, and landscape features that influence ice cover, are important in determining where eiders nest in Labrador. These results have fundamental implications for management of eiders populations and their nesting habitat in other northern areas. These findings also hint that in the future, climate change may play in changing the distribution and abundance of nesting eiders, suggesting that eiders maybe a candidate species for monitoring climate change impacts.

In the next Chapter I continue to investigate some important extrinsic factors such as relationships between eiders and sympatrically-nesting gulls. However I also explore intrinsic factors that may influence eider distributions. This is most plainly seen in patterns of local extinction and in the analysis of the intra-specific incidence and abundance curves. The primary idea behind these curves is that over time and in conjunction with many other factors; species may influence their own distributions, through dispersal and rescue effect. This in turn may feedback into patterns of abundance. For example, dispersed populations serve to decrease the risk of overall extinction by harboring source populations which may be unaffected by various negative forces (disease, predation, stochastic events). These source populations may allow individuals to disperse and re-colonize empty patches possibly thereby over time affecting overall abundance.

EXTINCTION, COLONIZATION, DISTRIBUTION PATTERNS AND NESTING ASSOCIATIONS OF EIDER AND GULL POPULATIONS IN LABRADOR

ABSTRACT: Extinction, colonization and distribution patterns were assessed within two families of migratory birds (Anatidae and Laridae). I used data collected during nest surveys for Common Eider (*Somateria mollissima*), Great Black-Backed Gull (*Larus marinus*) and Herring Gull (*L. argentatus*) on the Labrador coast between 1998 -2003. Data for both species of gull were pooled. For both eiders and gulls: small colonies were prone to extinction, mean abundance was a positive predictor of incidence, but colonization was not related to the measure of isolation used in my analyses. I also documented significant nesting associations, and found that gull colonies tended to track eider colonies across years. The overall observed extinction and colonization rates were: extinction = 0.08 and 0.23, colonization = 0.12 and 0.18, for eiders and gulls respectively, these rates showed substantial variation within and across archipelagos. My findings demonstrate previously unknown spatial and temporal population structure in Common Eiders and large gulls breeding in Labrador. Research into the trophic, landscape, genetic and behavioral mechanisms influencing these colonies would likely provide insight into the conditions and mechanisms that generated these patterns.

Andrewartha and Birch (1954) were among the first to recognize that many populations were discontinuous, often split by patchy environment resulting in multiple local populations. Subsequently, MacArthur and Wilson (1967) investigated the relationship between population turnover and community dynamics, followed by Levins

(1969) who developed a mathematical model to explain patterns of local extinction. Since then ecologists have come to understand that spatial distribution, patchy environments, and population turnover have many fundamental implications for conservation ecology.

Populations that exhibit habitat patchiness; local population extinction; colonization from adjacent local populations; and limited population connectivity are often labeled metapopulations (Hanksi 1991). Metapopulation concepts have been widely applied (Gulve 1994, Hanski and Thomas 1994, Appelt and Poethke 1997, Barbraud et al. 2003), mainly to organisms with limited dispersal ability (Szacki 1999). According to Esler (2000) if a migratory bird species shows certain levels of spatial structuring and philopatric behaviours a metapopulation approach can be useful in describing their population dynamics.

Johnsgard (1979) lists six sub-species of Common Eider (*Somateria mollissima*) Of these only four regularly breed in Canada: and only the American (*S. m. dresseri*), and northern (*S. m. borealis*) sub-species breed in Labrador (Mendall 1980, Knapton 1997, Goudie et al. 2000). While the existence of sub-species remains controversial (Zink 2004), there is substantial morphological variation in Common Eiders nesting across North America (Mendall 1980, Knapton 1997, Goudie et al. 2000). The existence of sub-speciation in Common Eiders at large geographic scales implies limited mixing across the species' range (Wright 1940), which in turn is consistent with metapopulation assumptions (Hanski 1991), albeit at large spatial scales.

Based on the presence of two sub-species in Labrador and the subsequent inference that these populations are not completely panmictic; the spatial structuring of

nesting islands at the local level (Chaulk et al. 2005a); female philopatric behaviors (Coulson 1984, Goudie et al. 2000) reaching as high as 98% in the Netherlands (Swennen 1990); and apparent local colony extinctions (K. Chaulk personal observation); I hypothesized that Common Eiders breeding in Labrador could be described using a metapopulation approach. Further, given that Great Blacked-Backed Gulls (*Larus marinus*), and Herring Gulls (*L. argentatus*) often nest with Common Eiders (Bourget 1973, Götmark and Åhlund 1984, Gerell 1985, van Dijk 1986, Götmark 1989, Swennen 1989, Mawhinney et al. 1999), I considered that these nesting associations might result in similar population processes for larids.

This chapter makes use of data collected during nest surveys to investigate population turnover and spatial distributions in common eiders and large gulls breeding on the Labrador coast. I predicted that eider and gull nesting associations would be higher than expected by chance, and that local nesting populations of eiders and gulls would exhibit features such as local colony turnover, and positive intraspecific incidence abundance curves. The existence of local colonization and positive incidence and abundance relationships would be considered evidence for rescue effect (Brown and Kodric-Brown 1977) from adjacent populations, rescue effect is one of the cornerstones of modern metapoplation theory (Hanski 1999)

STUDY AREA

Archipelagos near the communities of Nain and Hopedale were surveyed six times from 1998-2003. The archipelago adjacent to the community of Makkovik was surveyed once in 1999, and the one near Rigolet was surveyed four times from 2000-2003 (Figure. 6.1). The extent of the Nain study area was approximately 3383 km^2, containing

1000 islands ranging in size from 0.01 – 44800 ha. The extent of the Hopedale study area was approximately 566 km^2, containing 650 islands ranging in size from 0.01 – 3875 ha. The extent of the Makkovik study area was approximately 763 km^2, containing 300 islands ranging in size from 0.01 – 3396 ha. The extent of the Rigolet study area was approximately 2834 km^2, containing 335 islands ranging in size from 0.02 to 5204 ha.

All archipelagos shared similar environmental characteristics, including northern maritime climate, vegetation composed primarily of mosses, lichens, forbs, grasses and sedges. The archipelagos of Nain, Hopedale, Makkovik, and Rigolet were typically comprised of barren islands with sparse vegetation and very limited nesting cover. All four archipelagos are classified as coastal barrens (Lopoukhine et al. 1978) and are considered to have a high-boreal ecoclimate (Meades 1990) and a Low Arctic oceanographic regime (Nettleship and Evans 1985).

METHODS

Archipelagos were surveyed for evidence of breeding eiders and gulls, geodetic information from these surveys were plotted on 1:50000 digital base maps, and linked to tables containing information on species occurrence, nest abundance and density. In all areas, islands were selected for study based on random sampling (Chaulk et al. 2004, 2005a, 2005b). I limited my searches to islands that were estimated to be smaller than 30 ha. I did this for logistical reasons, as large islands require significant effort to search, so instead I focused on smaller islands that could be easily censused by small field crews over restricted time periods. Goudie et al. (2000) reported that Common Eiders preferred nesting on islands < 100 ha. Other researchers have used island size thresholds to help identify islands for investigation during eider breeding research (Nakashima & Murray

1988; Robertson & Gilchrist 1998; Merkel 2004) or focused on small islands during breeding surveys (Korschgen 1977; Gotmark & Ahlund 1984).

Ground censuses were conducted using standard search method employed by the Canadian Wildlife Service (Nettleship 1976) and other researchers (Falardeau et al. 2003, Merkel 2004, Chaulk et al. 2005a); these consisted of two to four people systematically walking over the islands searching for signs of eider nesting. Colony sizes were based on all detected nests (active, depredated, etc). Islands in the four archipelagos had limited cover and were for the most part barren, both hens and unattended nests were easily detected. In all cases an island colony was considered occupied if it contained at least one nest. The primary gulls nesting with eiders in the region were Great Black-Backed and Herring Gull, of these Great Black-Backed Gulls were more widespread. These two gull species were grouped to improve sample size for analysis. In addition these two gull species share a number of ecological similarities, in that they likely perceive eiders (eggs and ducklings) as a food source, and both species are likely to be perceived by eiders as predators.

Extinction and Colonization

To investigate extinction and colonization relationships I used Minitab 14 binary logistic regression, failure (extinction) or success (colonization) versus trial model (Minitab 2003). For both the extinction and colonization models, trial (or number of possible transitions) was equal to the number of survey years per island minus one. Extinction events were the change of an island colony from occupied to unoccupied from one survey to the next, though subsequent surveys did not always occur in successive years. Colonization events were a change of state from unoccupied to occupied. Failure was equal

to the number of extinctions, while success was equal to the number of colonizations. For the purposes of this paper, a colony is the number of nests on an occupied island, so a colony could consist of one nesting pair.

Only islands that were surveyed in two or more years were used in the analysis. Mean colony size was based on size of colony in years when birds were present. Isolation was quantified by creating 5 km buffers around each island and using Mapinfo 7.0 structured query language to determine the number of islands less than 30 ha inside this buffer. For the extinction model I used the following terms: species and log 10 of mean colony size nested within species. Terms for the colonization model included species and number of islands within a 5 km buffer nested within species. Colonization to extinction rate ratios were calculated using overall mean rates while the standard error of this ratio was calculated using the Delta Method (Williams et al. 2002). Extinction, colonization rates were compared using simple Z-tests (Pollock et al. 1990).

Incidence and Abundance

Two rectangular grid systems encompassing all four archipelagos were created in Mapinfo 7.0 using a spherical projection system (Figure. 6.2). The support or cell size (Perry et al 2002) of grid system one was 104 km^2; and for grid system two was 455 km^2. Structured query language was used to reduce each grid network to cells that contained surveyed islands. Cells containing fewer than three surveyed islands were not used in the analysis. The placement of each grid system was the same across all years.

Quadrats were created post hoc, after the island surveys were conducted. The initial positioning of each of the two grid systems was random. The size of the grid cells were determined based on the following criteria, they had to be large enough to include a)

at least 3 surveyed islands per grid cell and this determined the minimum size of the smaller grid network b) at least 12 grid cells per network, and this determined the maximum size for the larger network. The 3 islands per grid cell was to ensure the statistical minimum to calculate both the average and variance for incidence and abundance per grid cell. The 12 grid cell minimum per network was to ensure sufficient sample size for grid cell analysis. These two parameters set the limits for size of the grid systems and tended to work against each other.

Thus the lower limit for the smaller grid system was 90 km2 per grid cell. Using grid cells smaller than 90 km2 would mean that all grid cells would contain less than 3 sampled islands. The size of the cells of the smallest grid system was 10 km by 10 km, which is a simple rounded number that met the sampling basic criteria. But the 10 by 10 km grid system was created on a Euclidean surface, (i.e., a non projected computer matrix). When the grids were imported into a GIS they were distorted by the earth's imperfect curvature (which is non-euclidean), and by projection distortions which are common in mapping.

This meant the grid cells were slightly distorted from original size, the end result was the grid cells were about 104 km2 give or take 0.5 of a km2. This is acceptable since in mapping at the 1:50,000 scale lines edges are several meters wide. Taken across several kilometres on a rounded surface that is portrayed as a flat surface these distortions result in small deviations. These types of errors are well known and documented in cartography and in spatial ecology, it is the nature of mapping.

The larger grid system had the same basic criteria, accept that with the larger system the limiting factor was ensuring enough grid cells for analysis (N = 12). I found

the threshold here to be about 25 by 25 km or 625 km2 per grid cell. For example if the grid system was composed of one grid cell measuring 1000 km by 1000 km, it would have encompassed the entire study area, but with N = 1. In the end the maximum size of the larger grid network was rounded to 20 km by 20 km, or 4 times the size of the smaller grid network. However with the mapping distortions mentioned above the grid cells ended up being closer to 455 km2.

For this analysis trial was the number of surveyed islands in each grid cell, success was the number of trials when the relevant bird species was present. For example, suppose a grid cell had 6 surveyed islands, 4 of which were occupied by eiders for a total of 40 eider nests. For this cell, the incidence for eiders was 4/6 = 0.67, and the mean abundance was 40/6 = 6.7 eider nests/island. I used Minitab 14 binary logistic regression success and trial response procedure, which allows the use of ratio data (success/trial) to perform logistic regression, and a fully nested hierarchical model (Sokal and Rohlf 1995, Hosmer and Lemeshow 2000, Minitab Inc. 2003). Model terms included: species and year (main effects and interaction), archipelago nested within year, support nested within archipelago, and log 10 of mean abundance nested within support. As my data was inherently nested in structure (i.e., repeated measures, or colony counts, on the same islands over a six year period) I used a hierarchal nested model based on binary generalized linear modeling.

Eider-Gull Colony Relationships

Colony data were used to investigate breeding associations between eiders and large gulls. Trial was the number of survey years per island; success was equal to the number of trials that eiders were present. I used Minitab 14's binary logistic regression response and

trial procedure to test these associations with the following model: archipelago, gull presence nested within archipelago. I also ran a simple correlation to investigate the relationship between eider presence and gull presence.

Finally, I used simple two by two contingency tables to investigate the response of eiders and gulls to the presence or absence of the other in the previous breeding year (i.e. a Markovian process). I use the term tracking to describe the situation where a new colony was associated with the presence of another species the previous year. I conducted 4 tests to see whether: gulls tracked eider colonies, eiders tracked gulls, gulls abandoned eiders or eiders abandoned gulls, when they nested together in the previous year. Basically I used the model: presence/absence of eiders/gulls in year t versus presence/absence of eiders/gulls in year t+1.

General Statistics

When appropriate I present *P*-values for Hosmer-Lemeshow goodness of fit and actual Somer's D measure of association (Hosmer and Lemeshow 2000, Minitab Inc. 2003). The Hosmer- Lemeshow goodness of fit statistic assesses the fit of the logistic model against actual outcomes, and is a form of a Pearson chi-square statistic, $P > 0.05$ suggest that the model fits the data well (Peng et al. 2002). The Somer's D measure of association statistic evaluates how the predicted probabilities of the logistic model agree with the actual outcomes (Peng et al. 2002). Models terms were included because of significant relationships documented during earlier research (Chaulk et al 2004, 2005a, 2005b), or because the terms were required by my current hypothetical framework. All statistical tests were two-tailed and critical alpha was set at 0.05.

RESULTS

The relationship between colony size and extinction was negative for both eiders and gulls (Figure 6.3; $G = 52.99$, df = 3, $P < 0.01$, $\beta_{eiders} = -2.07 \pm 0.50$, Odds $Ratio_{eiders} = 0.13$, $\beta_{gulls} = -0.95 \pm 0.63$, Odds $Ratio_{gulls} = 0.39$, Hosmer-Lemeshow = 0.85, Somer's D = 0.38), so that large colonies were less likely to go extinct in subsequent years. With respect to colonization, the numbers of islands within a 5 km buffer was not a significant predictor of colonization rate ($G = 13.36$, df = 3, $P_{eiders} < 0.59$, $\beta_{eiders} = -0.00 \pm 0.01$, Odds $Ratio_{eiders} = 1.00$, $P_{gulls} = 0.31$, $\beta_{gulls} = -0.00 \pm 0.01$, Odds $Ratio_{gulls} = 1.00$, Hosmer-Lemeshow = 0.28, Somer's D = 0.24), suggesting that our measure of isolation of local populations was unimportant with respect to recolonization. Extinction ($G = 43.04$, df = 5, $P < 0.01$) and colonization ($G = 14.69$, df = 5, $P = 0.01$) rates also varied by archipelago and species (Table 5.1). Overall gulls had higher turnover rates than eiders ($Z_{extinction} = 2.12$, $P_{extinction} = 0.03$; $Z_{colonization} = 9.90$, $P_{colonization} < 0.01$) while eiders had a higher colonization to extinction (C/E) ratio ($Z_{c/e} = 3.37$, $P_{c/e} < 0.01$; Table 5.1). With respect to the incidence abundance curve, the global logistic regression model suggests that mean abundance (log 10) was a significant positive predictor of incidence for eiders and gulls at both spatial grains in all archipelagos (Figures. 6.4 and 6.5; $G = 361.54$, df = 69, $P < 0.01$, Hosmer Lemeshow = 0.88, Somer's D = 0.49), suggesting that with higher eiders numbers more islands were occupied..

Simple correlation (r = 0.84) and binary logistic regression analysis ($G = 88.12$, df = 7, $P < 0.01$, Hosmer Lemeshow = 0.23, Somer's D = 0.48) revealed that eider and gull presence were positively related, meaning that you were more likely to find these species co-nesting. Gulls preferentially colonized islands occupied by eiders the previous year ($\chi^2 = 6.07$, df =1, $P = 0.01$), while the converse was not significant. Neither eiders nor

gulls showed evidence of preferentially abandoning colonies when they were nesting sympatrically with the other species in the previous year.

DISCUSSION

Understanding local extinction and colonization dynamics is fundamental to conservation ecology and is essential for the development and implementation of long-term conservation plans. Taken out of context local extinction events can appear more negative and local colonization can appear more positive than they actually are for a given population or species.

During the study gull colonies were in a higher state of flux than eider colonies. Eiders also had a higher colonization to extinction (C/E) ratio than gulls. The relatively high rates of colonization and extinction that I documented are probably more typical of northern nesting birds, as colonies of all three species tend to be larger (100s – 1000s of pairs) with fewer overall colonies in temperate climates. This difference in colony size may simply be a function of landscape, where Labrador has thousands of islands on which marine birds can chose to nest (Chaulk et al. 2004), and more southern archipelagos may be less complex and offer fewer choices for colony selection.

My analysis suggests that colony size is a significant negative predictor of local extinction for both eiders and gulls. In earlier research over the same time period, I documented significant population increases of Common Eiders in Labrador (Chaulk et al. 2005b). There is also evidence of population declines of large gulls breeding in Newfoundland, Labrador and eastern Hudson Bay (Gilchrist and Robertson 1999, Robertson et al. 2001, 2002). The colony turnover findings are consistent with these general trends, as one would expect to find larger C/E ratio in a growing population.

While researchers have investigated colony site dynamics in some colonial bird species (Erwin et al. 1998, Barbraud et al 2003) there seems to be limited information available on eider-gull colony turnover rates relative to population growth upon which I can make comparisons. I recommend the relationship between local extinction, colonization and overall population growth as a topic of future investigation.

I also investigated the effect of geographic isolation on colonization rates. The findings revealed that this relationship was not significant, though this may have been due to the isolation measures I used in the analyses. For example, I had incomplete knowledge of all colony locations; instead I counted all islands less than 30 ha within a given radius of each surveyed island. Many of the islands captured by this method may have been unsuitable and could have biased the analysis. In addition the dispersal ability of migratory birds is so vast that larger spatial scales (100's km^2) maybe required to detect relationships between colonization and isolation. Conversely site tenacity may be so high, that much smaller spatial grains are needed to detect relationships between isolation and colonization. Future work could include mapping all known colonies within these archipelagos, calculation of nearest neighbour distances with subsequent re-investigation of the colonization isolation relationship.

Many species have been shown to have positive incidence (distribution) and abundance relationships (Hanski 1982, 1999, Nee et al. 1991, Gaston and Curnutt 1998) and there is a growing body of research that explores this phenomenon (Bock and Ricklefs 1983, Brown 1984, Wright 1991,Gaston and Blackburn 1996, Gaston et al. 1997, Johnson 1998, Venier and Fahrig 1996). The importance of distribution and abundance relationships are often over looked. Gaston and Curnutt (1998) found that within the

common grackle (*Quiscalus quiscula*) distribution increased as the population declined. In contrast as the Northern Cod (*Gadus morhua*) population declined, both the fish and the fishermen aggregated, keeping catch rates high. Seeing no change in catch rates, quotas remained constant and the northern cod population collapsed due to over fishing (Rose et al. 1993). These examples demonstrate the variability in the distribution and abundance relationship as well as the importance of simultaneous consideration of distribution and abundance in the management and conservation of natural resources.

One of the leading explanations for the positive intra-specific incidence and abundance curve is rescue effect from adjacent local populations (Brown and Kodric-Brown 1977). Although niche breadth, sampling errors and habitat availability have also been suggested as potential causes (Brown 1984, Wright 1991, Venier and Fahrig 1996). The data suggest that Common Eiders and large gulls nesting in Labrador exhibit positive intra-specific incidence abundance curves. I found that this pattern of incidence and abundance repeated at two spatial scales. This is an important finding given the large volume of ecological texts and literature that stress the importance of pattern assessment at multiple scales (Weins 1989, Levin 1992, Schneider 1994, Turner et al. 2001, Scott et al. 2002).

I have no data on movement patterns within or across archipelagos for either gulls or eiders breeding in Labrador, and I was not able to demonstrate a relationship between isolation and colonization. In the case of breeding Common Eiders, some researchers have documented extremely high rates of philopatry (Swennen 1990), and a strong tenacity to brood rearing areas (Bustnes and Erikstad 1993). While other researcher have shown have suggested that eiders do occasionally move between adjacent colonies across

breeding years (Milne 1974, Schamel 1977, Mehlum 1991, Merkel 2004). These information sources suggest that breeding eiders have strong philopatric tendencies to either islands or island clusters, supporting the idea of local population structure and limited population mixing across large spatial scales. It seems likely that there may be several levels of spatial structuring for common eiders including: sub-species, regional level structure (i.e, across archipelagos), and within archipelago (across colony). Meanwhile, research into dispersal patterns is essential for a complete understanding of spatial population processes, and is suggested as a topic for future research. In the interim, I interpret the positive intra-specific incidence abundance curve as indirect evidence of connectivity and rescue effect.

Ecological studies commonly investigate extrinsic factors that influence either the distribution and/or abundance of organisms. Common Eiders and large gulls species often nest together and both species are known predators of Common Eider eggs and young. Great Black-Backed and Herring Gulls are thought to mate and occasionally produce hybrid offspring (Rooke 1961, Jehl 1960, Andrle 1972, Good 1998). Some researchers have suggested that eiders receive benefits by nesting with large gulls (Gerell 1985, Swennen 1989) while others suggest that such nesting associations are costly (van Dijk 1986) or of no benefit to eiders (Götmark and Åhlund 1984). I feel that the approach of pooling the two gull species together is warranted given the fact that the interaction between Herring Gulls and eiders and Great Black-Backed Gulls and eiders is likely to be similar, in that both prey on eider nests, although realistically predation rates may vary between the two species. I recognize that there may be intraspecific differences in the population processes of these two larids, and therefore I suggest that future studies

attempt to resolve these potential differences. It should be noted that we have no information relationships between eiders and other gulls species nesting in the study area.

The data suggest that eiders and gulls are more likely to co-nest than expected by chance. The analysis of the effect of colony composition from one year to the next suggests that gull colonies track eider colonies across time (i.e., a Markovian process). I am uncertain why these patterns occurs, but expect that this interaction is very complex because in Labrador and elsewhere, Great Black-backed Gulls and Herring Gulls usually initiate nesting before eiders. It may be that eiders and gulls may be drawn to similar environmental characteristics (avoidance of mammalian predators, proximity to food), nest together because of predator prey relationships (van Dijk 1986), or commensal relationships. Eiders visit nesting islands before nesting is initiated (Goudie et al 2000) and gulls may use eider presence to identify potential nest colonies within a given year. Based on nesting chronology, eiders could avoid gulls within a year but given the high nesting association levels it appears that any within year gull avoidance strategy (if one exists) is ineffective; furthermore my analyses suggest that eider colonies do no relocate to avoid gulls across subsequent years. Since eiders have high levels of site tenacity gulls may exploit this behaviour when selecting islands on which to nest. More research is required into this important relationship, and could include banding and observational study, and tracking eider nest success on islands shared with gulls and on islands where no gulls are present.

Patterns in the distribution and abundance of animals occur because of various intrinsic (dispersal, philopatry, conspecific attraction) and extrinsic mechanisms (food, predator responses, disease, landscape features, climate, etc). A variety of theories,

models, and hypotheses have been developed to describe spatial population structure (Levins 1969, Fretwell and Lucas 1970, Pulliam 1988, Stamps 1988). The spatial structure of nesting islands, patterns of extinction and colonization, and a positive intraspecific incidence abundance curve lead us to conclude that concepts derived from the metapopulation framework, such as colony level colonization, extinction and incidence-abundance curves can be usefully applied to eider populations breeding in Labrador. While I documented similar population processes in large gulls, because my data was pooled I feel that additional research on the population structure and colony dynamics of each individual gull species is necessary.

Though particular metapopulation characteristics or even the metapopulation label can be argued, it is clear that a comprehensive understanding of population dynamics can only be achieved by simultaneous consideration of space and time. My findings support the notion that highly mobile organisms such as migratory birds can be described using characteristics associated with metapopulation structure and function. I suggest that conservation planners dealing with these bird groups consider metapopulation or other spatially explicit models to assist in developing ecologically relevant conservation strategies, such as protecting networks of islands that will sustain local population processes.

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Table 6.1. Observed local colony extinction and colonization rates (mean ± 1 SE) for Common Eiders and large gulls (Great Black-backed and Herring Gulls), on the Labrador coast, 1998-2003. C/E ratio is colonization rate divided by the extinction rate.

	Rate	Nain	Hopedale	Rigolet	Overall
No. Islands		39	62	24	125
No. Trials		112	177	35	324
Common Eider	Extinction	0.05 ± 0.01	0.13 ± 0.01	0.02 ± 0.01	0.08 ± 0.01
	Colonization	0.12 ± 0.04	0.13 ± 0.03	0.10 ± 0.06	0.12 ± 0.02
	C/E ratio	2.40 ± 0.16	1.0. ± 0.24	0.5 ± 0.16	1.50 ± 0.14
Large Gulls	Extinction	0.22 ± 0.01	0.29 ± 0.01	0.09 ± 0.01	0.22 ± 0.01
	Colonization	0.23 ± 0.04	0.15 ± 0.03	0.17± 0.06	0.18 ± 0.02
	C/E ratio	1.05 ± 0.17	0.52± 0.39	1.89 ± 0.20	0.82 ± 0.15

Figure. 6.1. General location of archipelagos surveyed for Common Eider and large gull nests between 1998-2003 on the Labrador coast.

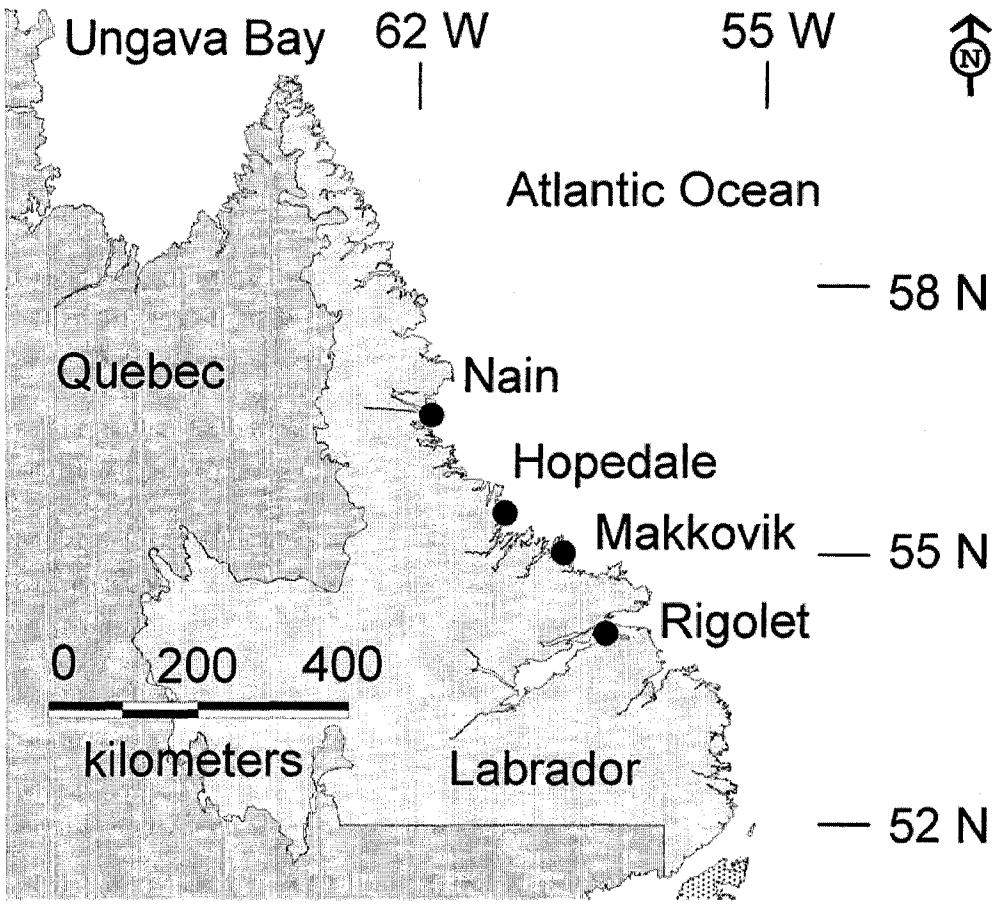


Figure. 6.2. An example of the grid systems used in the incidence abundance analysis, based on surveys of the Nain archipelago in the year 2000. The figure shows a subset of grid system one (support = 104 km^2), and shows cells that contain surveyed islands.

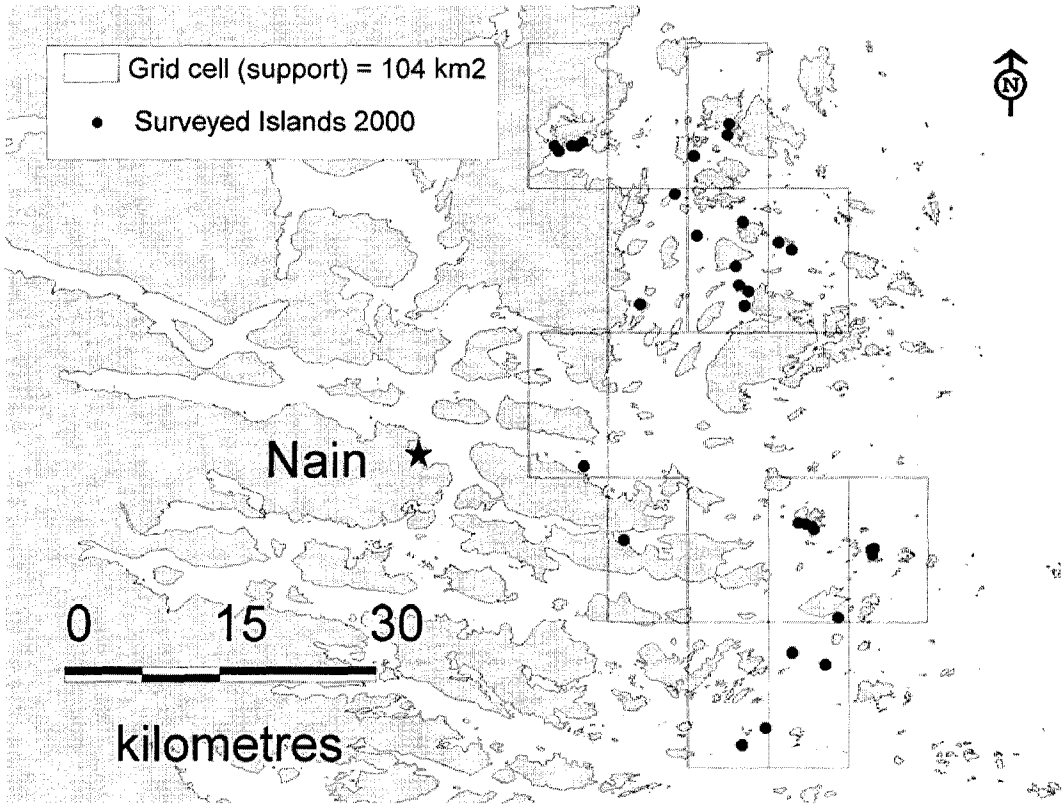


Figure. 6.3. Observed colony extinctions and mean colony size of Common Eiders and large gulls (with data for Herring and Great Black-backed Gulls pooled) breeding in Labrador, 1998-2003. Model used log 10 of abundance as predictor.

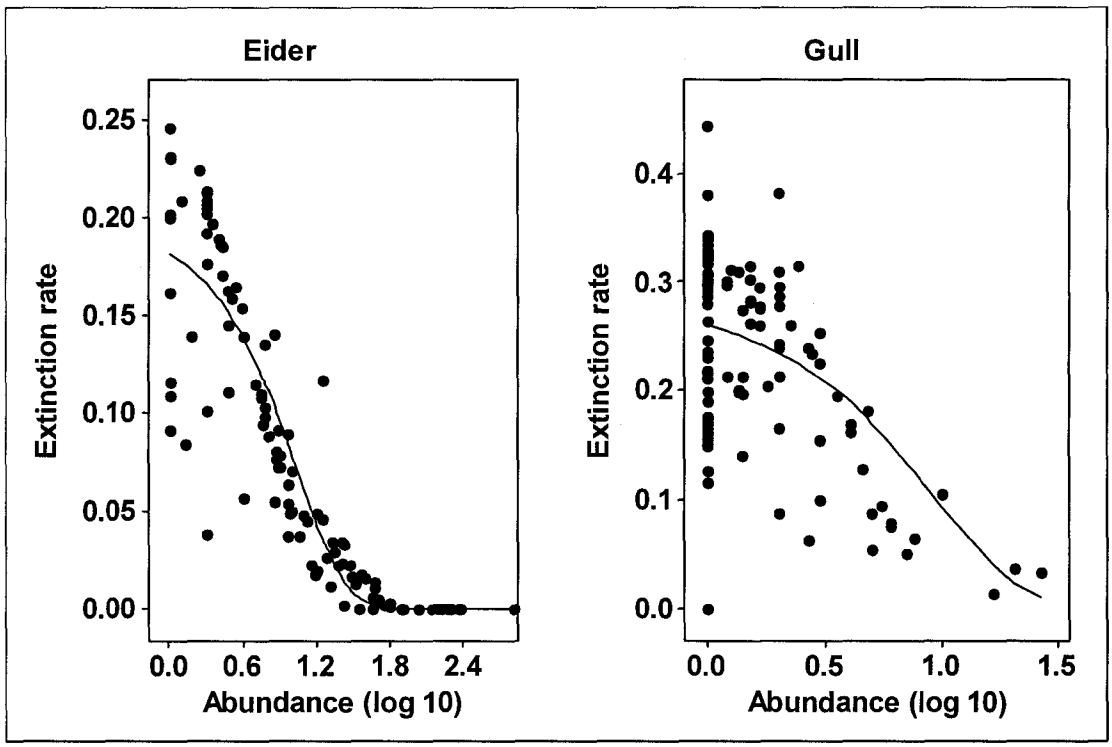


Figure. 6.4. Intraspecific incidence abundance curve for breeding Common Eiders on the Labrador coast, 1998-2003. Two spatial scales were investigated; one grid cell size (support) was 104 km^2, and the other 455 km^2. Mean abundance is total number of nests per grid cell divided by number of islands surveyed.

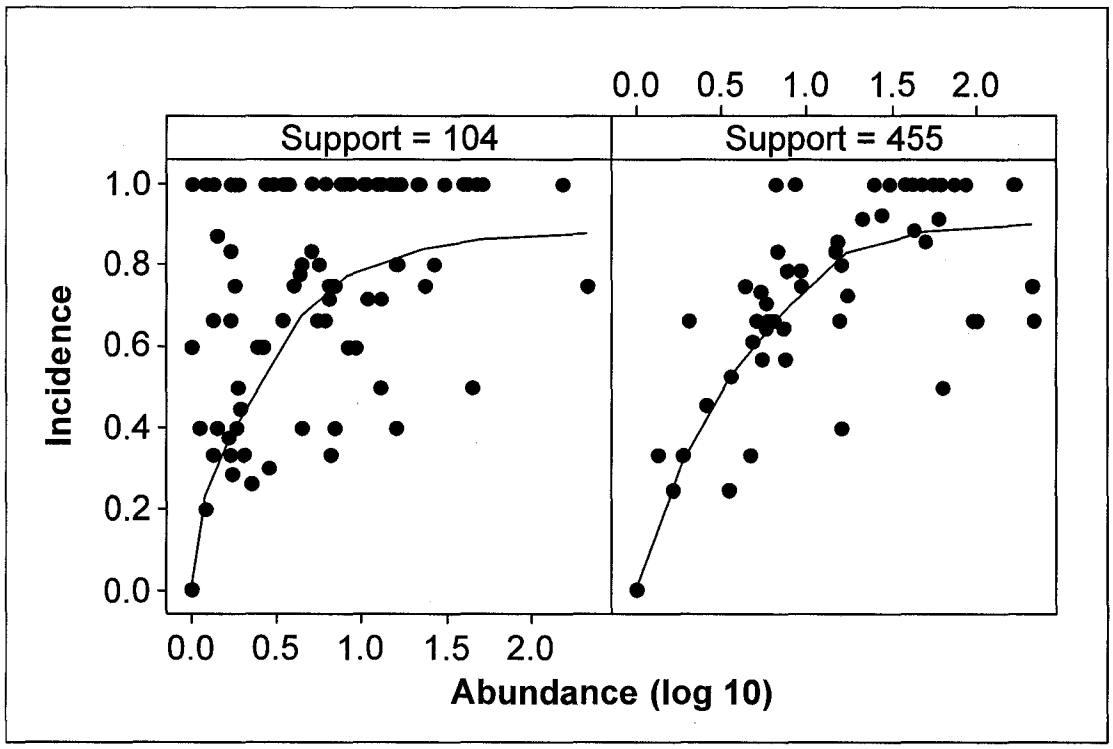
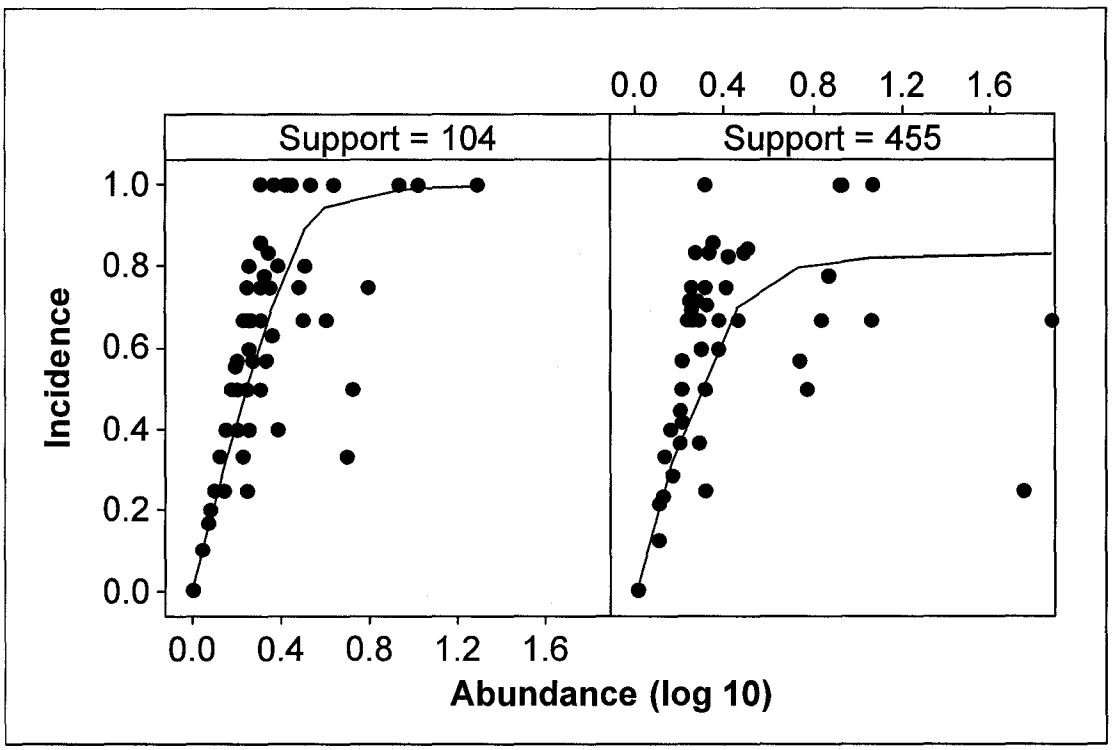


Figure. 6.5. Incidence abundance curve for breeding Great Black-backed and Herring Gulls on the Labrador coast, 1998-2003. Two spatial scales were investigated; one grid cell size (support) was 104 km^2, and the other 455 km^2. Mean abundance is total number of nests per grid cell divided by number of islands surveyed.



CHAPTER TRANSITION

In this chapter I found that eider distributions and their abundance were indeed related, suggesting some rescue effects may be at play. Supporting this notion, I also found a strong relationship between eider colony size and the probability of colony extinction. Overall, eider colonies in Labrador showed significant turnover, with colonization events being particularly frequent (and consistent with the evidence in Chapter 4 that the populations are increasing). This high level of redistribution of eider colonies is consistent with the result that ice cover is an important determinant of eider abundance and distribution, as ice cover is both spatially and temporally variable. Relationships with gulls were weaker, but it appeared that gull colonies tracked eider distributions, rather than other way around. In the next and final chapter I discuss all my findings and attempt to integrate them within various theoretical contexts while addressing the primary thesis question(s).

CONCLUSION

My primary research interest is in understanding the spatial distribution of organisms. This document synthesizes my ideas on the distribution and abundance of nesting eiders in Labrador. I engaged this topic by asking why eiders nests where they do? This thesis was written in manuscript format and most of the research chapters have been published or submitted for publication. The very nature of publication in scientific journals requires that manuscript have a tight and narrow focus, plus the journal review process will often take papers in slightly different directions. So while there are benefits to writing a thesis in journal format (i.e., ease of publication), there are drawbacks (the general theme of the dissertation may be somewhat obscured). In this the final chapter, I review specific findings of each chapter, relate them to the larger theoretical framework, and more specifically attempt to answer the question why eiders nest where they do?

Chapter Results

Historically, eider research in Labrador has been sparse relative to other regions within the species' global range. Data and conclusions in my thesis provide some of the first published information on basic eider nesting biology and ecology and population dynamics for Labrador. In Chapters 2-3, I document numerous reproductive parameters (such as nest initiation, clutch size, nest density, etc.), outline regional and annual differences in distribution and abundance, and in Chapter 4 I document population trends of eiders between 1998 - 2003.

My data on population structuring (Chapter 2) has considerable potential value from both academic and applied perspectives. Population structuring is an important component in evolution (Wright 1940). Johnsgard (1979) lists six sub-species of

common eider; only the southern (*S. m. dresseri*) and northern (*S. m. borealis*) sub-species breed in Labrador (Mendall 1980, Goudie et al. 2000). However, the area of overlap between the southern and northern eider sub-species was poorly known. Multiple lines of evidence (provided in Chapters 2 and 3) suggest that eiders nesting from Nain north belong to the northern sub-species; eiders nesting in and south of St. Peter's Bay belong to the southern sub-species. Eiders that nest between these two areas are likely to be mixed (individuals present from both the northern and southern sub-species or hybrids). These findings are interesting in their own right and because hybrid zones are important in micro-evolutionary research.

My findings also have implications for conservation. For example, the presence of distinct population units provides a strong argument for the implementation of different geographically-based management regimes. Yet, my findings suggest similar population trends in both the northern and southern sub-species. Therefore, current management strategies that do not differentiate between the two sub-species in Labrador, are not necessarily having adverse effects. In fact there is good anecdotal evidence that past management practices (e.g. bag – season restrictions) have aided population growth. The data presented here are timely and will aid in the co-management of eiders in Nunatsiavut, the new Labrador Inuit land claim area. These data will also help regional, national and international agencies in harvest planning and help guide international eider conservation efforts.

In Chapters 5 and 6, I investigated population structure at smaller spatial scales (islands and grids) and identified important habitat features that could advance understanding of spatial population dynamics. I presented data that could have direct and

indirect theoretical implications that transcend taxonomic boundaries. In Chapter 5, I explored the role of food, landscape, ice, and how these affect eider distribution and abundance. Many models explain distribution patterns in colonial birds, some of these do so by linking food availability and prey depletion to population regulation and colony dispersion (e.g. Asmole 1963, Furness and Birkhead 1983, Birt et al. 1987, Cairns 1989). My findings, however, suggest that the amount of intertidal prey adjacent to colonies is of limited importance to nesting eiders. This finding was supported when I demonstrated that shallow subtidal areas, which should theoretically be important as foraging areas, did not translate into greater eider abundance. Both lines of evidence suggest that forage may be less important than other habitat features when eiders select islands on which to nest.

In Chapter 5, I hypothesize that during the spring, areas with high island density trap pack ice and thus provide bridges for mammalian predators to nesting islands. Analysis of ice and landscape supported this contention, although we did not investigate predation rates directly, areas with more islands do trap ice, which will serve as bridges for predators thereby increasing access to nesting islands by terrestrial predators. This relationship is expected to be highly sensitive to climate change and carries implication for climate change research.

As noted above, I did not investigate mammalian predation directly, but many researchers have suggested that mammalian predators influence eider-nesting behaviour (Larson 1960, Quinland and Lehnhausen 1982, Robertson 1995, Quaken–bush and Sudyam 1999, Goudie et al. 2000). On the Labrador coast, terrestrial predators can decimate entire nesting colonies (Chaulk unpublished). My findings on the relationship between landscape pattern and colony size and distribution are consistent with Huffaker's

(1958) seminal research on population distributions which in turn had significant influence on the development of original metapopulation theory by Levin (Hanski 1999). My landscape findings provide an important validation of the metapopulation model presented in Chapter 6, which hopefully can be generalized to other species.

In Chapter 6, I look at several important intrinsic and extrinsic factors which influence the distribution and abundance of nesting eiders. Relationships between nesting eiders and nesting gulls are explored. In addition I look at patterns of extinction, colonization, and incidence and abundance relationships in both groups. Many of these topics (patchy distributions, local population turnover, distribution and abundance relationships) are derived from metapopulation theory. To date, metapopulation concepts have been applied to organisms with limited dispersal ability (Szacki 1999). The present demonstration (and others, e.g. Esler 2000) is helping to break down conceptual barriers and to document the applicability of metapopulation processes to migratory bird ecology. This expansion of the taxonomic and behavioural boundaries of metapopulation theory will facilitate wider application of metapopulation concepts and in turn could hold implications for conservation and theoretical ecology. In addition these findings provide insight into some of the factors which do (and don't) influence the spatial distribution of nesting eiders.

Theoretical Implications

In my approved thesis proposal of March 2003, I originally considered a variety of theories and models to describe spatial population structure of nesting eiders including: the Dynamic Theory of Island Biogeography (MacArthur and Wilson 1963, 1967), Metapopulation Theory (Levins 1969, Hanski 1999), the Ideal Free Distribution (Fretwell

and Lucas 1970), Adaptive Deme Formation Hypothesis (Edmunds and Aalstad 1978), Niche Breadth Hypothesis (Brown 1984), Source-Sink Population Dynamics (Pulliam 1988) and Conspecific Attraction (Stamps 1988).

Of these metapopulation theory, the ideal free distribution and ideal preemptive distribution, and conspecific attraction seemed to be the most likely to apply to nesting common eiders. In the next four sections I provide summaries of these models along with the *a priori* hypotheses that were developed in the thesis proposal. It should be noted that some of these theories are not directly discussed in the data chapters. The reason for this is related to publication effort in that I some times I used a limited and narrow focus to expedite the publication of each chapter. This is especially true for Chapters 2 and 3. In hindsight it might have been better for these papers to have explicitly discussed theoretical contexts such as the ideal free distribution or the ideal preemptive distribution. Because this was not done, or in some cases fully developed, I use this final chapter to clearly develop the links between research chapter and the primary thesis question.

Ideal Free Distribution

About one year after the basic metapopulation concepts were introduced, Fretwell and Lucas (1970) reviewed the assumptions and predictions of various models related to the distribution of animals and habitat. One of these models, the Ideal Free Distribution (IFD) held that individuals of a species will distribute themselves in response to the habitat characteristics of their environment (Fretwell 1970, 1972, Bernstein et al. 1991). Many of the assumptions of IFD have been relaxed in recent years (Poysa et al. 1998). The original IFD makes a series of assumptions, some of which are naïve: individuals have complete knowledge about the profitability of resources; individuals are alike

genetically; all individuals are equal competitors; individuals occupying a habitat patch have similar success rates; individuals settle in suitable habitats first; individuals are free to enter any habitat. Meanwhile other assumptions of IFD are more realistic: habitat suitability is assumed to be highest at zero density (Fretwell and Lucas 1970).

If eider nesting follows the patterns predicted by the ideal free distribution, then fitness (or a correlate of fitness) should be equal between different areas. Therefore clutch size (a correlate of fitness) should be the same regardless of nesting area (i.e., between islands and between archipelagos). In my thesis proposal I developed the following *a priori* null hypotheses: H_o) average clutch size will be equal between breeding areas. My findings with respect to clutch size (Chapters 2 and 3) led me to reject this null hypothesis. Therefore, I conclude that the IFD may not be an applicable framework with which to investigate eider population processes.

Ideal Preemptive Distribution

Nearly 20 years after Fretwell and Lucas (1970), Pulliam (1988) presented a model whereby birth and death rates varied by habitat, subsequently this concept has become known as source-sink population dynamics. In a source area, birth rate exceeds death rate, while the opposite occurs in a sink (Pulliam 1988). Source habitats are exporters of individuals, these individuals migrate to sink habitats following similar processes outlined in the Ideal Free Distribution (Pulliam 1988). Pulliam and Danielson (1991) expanded the source-sink model and suggested that habitat induced demographic differences could result in spatial population structure. Pulliam and Danielson (1991) proposed the Ideal Preemptive Distribution (IPD) as a more realistic alternative to IFD to explain apparent patterns of habitat selection.

IPD incorporates individual differences in reproductive success (Poysa et al. 1998, Pulliam and Danielson 1991). IPD predicts that average reproductive success of individuals in habitat 2 will be less then in habitat 1 (Pulliam and Danielson 1991). Furthermore the number of individuals occupying habitat 2 is less than predicted by the Ideal Free Distribution (Pulliam and Danielson 1991). According to IPD areas with higher fitness (i.e., sources) typically have higher population density, but under certain conditions sinks could have higher population densities (Pulliam 1988). The latter scenario (i.e., sinks with higher population) is unlikely in real world situations (Pulliam 1988).

IPD predicts that some habitats will have higher densities than others and that these differences will vary based on habitat suitability. In my thesis proposal, I developed the following *a priori* null hypothesis H_o) there will be no relationship between nesting abundance and habitat quality. My findings with respect to nest density (Chapters 2 and 3) and habitat (Chapter 5) lead me to reject this null hypothesis. Therefore, I conclude that IPD may be an applicable framework with which to investigate eider population processes.

In order to test IPD, information on the average reproductive success of individuals in each habitat and knowledge of breeding site quality is required (Pulliam and Danielson 1991). Therefore more appropriate null hypothesis could have been used such as: H_o) Nest success (fitness) will have no relationship with habitat quality. However, I lacked the resources to test this hypothesis directly. Instead, I used nest abundance/density as a proximate correlate of source-sink distribution patterns.

Assuming that greater nest success leads to higher local densities, findings in Chapters 2, 3, 5, and 6 can be taken as indirect evidence that IPD could apply to eider distributions.

Conspecific Attraction

Stamps (1988) hypothesized that conspecific attraction (CA) could occur in migratory birds breeding at high latitudes. Under the CA hypothesis, individuals use conspecifics as indicators of habitat quality (Poysa et al 1998, Stamps 1988), or produce benefits related to mating success and predator defence (Poysa et al 1998). Given that eiders are social (Chapedelaine et al 1986, Schmutz et al 1983), I decided to consider the CA hypothesis as a potential factor influencing the spatial ecology of nesting common eiders. In my thesis proposal, I developed the following *a priori* null hypotheses: H_o) If eiders distribute themselves randomly among islands then the variance to mean ratio (also known as the coefficient of dispersion, CD) should equal one. My findings with respect to the coefficient of dispersion are vague, in that the coefficient of dispersion appears to change depending on landscape features (Chapter 5). I also developed a second null hypothesis in my thesis proposal: H_o) If eiders distribute themselves randomly among islands then expect an Incidence and Abundance curve (IA) with slope equal to zero. My findings with respect to incidence and abundance led me to reject this null hypothesis (Chapters 5 and 6). I conclude that conspecific attraction may be an applicable framework with which to investigate eider population processes, but that further exploration of these findings are needed.

Metapopulation Theory

Levins (1969) proposed a mathematical model to explain patterns of local extinction and colonization in pests. The metapopulation model has since grown to deal with patchy

habitat, colonization, extinction, isolation, rescue effect, as well as distribution and abundance relationships (Hanski 1999). A metapopulation can be described as a population of populations (Hanski 1991) and common assumptions include: habitat patchiness; local population extinction; colonization from adjacent local populations; and population connectivity without complete mixing (Hanski 1991). Modern metapopulation theory predicts that occupancy and average colony size are negatively related to isolation, resulting in a positive intra-specific IA curve (Hanski 1982, 1999). The IA curve describes the relationship between the average size of existing populations versus population distribution, for example within a given area patch occupancy and average size of local populations will be positively related. It should be noted that the existence of a positive IA curve does not necessarily imply metapopulation structure (Hanski 1999), since positive IA curves can be explained by other mechanisms, including naturally occurring yet random patterns (Gaston et al. 2000, Wright 1991, Taylor 1961), aggregated resources (Gaston et al. 1997), habitat relationships (Venier and Fahrig 1998) and/or the niche breadth hypothesis (Brown 1984). However, the absence of a positive IA curve would imply that metapopulation structure is unlikely (Hanski 1999). Metapopulation theory also predicts that extinction is negatively related to colony size.

If eider nesting follows the spatial distribution predicted by metapopulation theory then the number of occupied islands within a patch should be positively related to average colony size within that patch (i.e., a positive IA curve), and eider colony size and extinction rate should be negatively related. In my thesis proposal, I developed the following a priori null hypotheses: H_0) There is no relationship between the number of occupied islands and colony size within a given area. My findings with respect to

incidence and abundance (Chapters 5 and 6) lead me to reject this null hypothesis. In my thesis proposal I also developed a second null hypothesis: H_o) There is no relationship between extinction rate and colony size. My findings with respect to colony size and extinction (Chapter 6) lead me to reject this null hypothesis. Therefore, I conclude that metapopulation theory may be an applicable framework with which to investigate eider population processes.

Synthesis of Findings

With respect to the primary research question of this thesis: why do eiders nest where they do? I found that three major theoretical frameworks (metapopulation, IPD, and conspecific attraction) were supported. In some cases, this is not surprising. For example, since source-sink population dynamics have been integrated into metapopulation theory (Hanski 1999). Also that eiders did not follow the Ideal Free Distribution is not surprising since IFD is mainly viewed as a null model for testing purposes.

It should be noted however that source-sink population dynamics and conspecific attraction are sometimes thought to be mutually exclusive (Poysa et al 1988). My results indicate that these two models may not be mutually exclusive with respect to eiders. This could be due to the fact that eiders are facultative in their colonial behaviour. Thus, a continuum of mutual exclusivity between source-sink and conspecific attraction models might be expected depending on the level of colonial behaviour. All four major models attempt to describe distribution patterns, and my findings imply that most of these might apply to spatial dynamics of eider nesting ecology. This suggests that greater effort needs

to be placed on integrating these models into a more unified theoretical context to explain distribution and abundance.

Findings on population trend (Chapter 4) were not directly related to any of the theoretical contexts discussed in this thesis, but it is important to realize that population instability could have influenced my overall results and assessment in some unknown fashion. Therefore the findings presented in this thesis must be interpreted knowing that eider populations were increasing. With respect to Chapter 4 and the rest of the thesis, I have come to believe that it may be possible to model trends in incidence and abundance (IA), and that IA trends may have similar relationships as the instantaneous intraspecific IA relationships I documented in Chapters 5 and 6. While investigations of IA trends were beyond the scope of this thesis, if this is true I believe it could open a new door for monitoring animal populations that occur in discrete and/or patchy space. For example, it is often easier to document the presence or absence of an animal than it is to count individuals. A known relationship between incidence trend and population abundance trend would reduce field work and make monitoring efforts easier, and less expensive. Therefore allowing resource managers to increase the number of monitored species, and thereby adding to our overall understanding of ecosystem change.

Why do eiders nest where they do?

Many factors play a role in determining why eiders nest where they nest. These relate to inter-specific interactions (Chapter 5 and 6), conspecific attraction (Chapter 5), landscape features (Chapter 5), rescue effect and core satellite processes (Chapter 5 and 6) and abiotic factors (Chapter 5). In addition, commensalism (Chapter 6) and more importantly predation (Chapter 2, 5, 6), also seem to play roles. Interestingly, my

findings suggest that food does not play a role in determining why eiders nest where they do, or if it does it is masked by other processes such as prey depletion, or as a result of survey methodology. Johnson and Krohn (2002) studied the habitat requirements of eiders and found that cover and disturbance were important. In northern Labrador, eiders nest on barren islands and cover is not likely to play a significant role, since it is missing from most habitats. However, it does seem likely that disturbance probably does play a large role in nest success, although I did not investigate this directly. In Chapter 4, I noted that the collapse of the inshore fishery coincided with the start of population increases, again disturbance and reduction in hunting may have played a role (see Chaffey 2004).

SUMMARY

To summarize, I documented spatial population structure at different scales (island, island cluster, archipelago, etc.), observed population increases, as well as patterns in local extinction and colonization. Extinction and population trends are at the very core of conservation ecology. Through understanding of local processes, I hope that we can better understand regional and global processes, and perhaps address mechanisms of large scale spatial population dynamics. In turn, I hope that we will be able to better determine when and what actions are required for conservation and management and act accordingly.

At a theoretical level, my findings suggest that future research in spatial ecology should focus on synthesizing competing distribution models into a general unified theory of distribution and abundance. This is a daunting task and, given the complexity of modeling ecological systems, will likely require the combined multi-disciplinary efforts

of experts from many fields, including behavioural, population, spatial and theoretical ecology, genetics, mathematics, computer programming and geography. In particular, the Ideal Free Distribution and Conspecific Attraction Hypotheses need to be incorporated in metapopulation models, in the same manner that source - sink population dynamics (Pulliam 1988) have been (Hanski 1999), so that metapopulation concepts can be broadened. Efforts need to be made to outline how each of the remaining theories relate to each other, and whether any new predictions arise as a consequence of this synthesis. This endeavor is beyond the scope of this dissertation, but will hopefully be facilitated by it.

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APPENDIX A: Coordinates of Islands Surveyed. Coordinates in Decimal Degrees, North American Datum 1983.

ID	ARCHIPELAGO	LONGITUDE	LATITUDE
DUK01	HOPEDALE	-60.23930	55.36230
DUK02	HOPEDALE	-60.27040	55.32210
DUK03	HOPEDALE	-60.27300	55.32920
DUK03.5	HOPEDALE	-60.27440	55.32900
DUK04	HOPEDALE	-60.28010	55.31430
DUK05	HOPEDALE	-60.30780	55.30100
DUK06	HOPEDALE	-60.30760	55.22910
DUK07	HOPEDALE	-59.91530	55.53010
DUK08	HOPEDALE	-59.92850	55.53400
DUK09	HOPEDALE	-59.95660	55.52820
DUK10	HOPEDALE	-59.92440	55.53790
DUK100	HOPEDALE	-60.26840	55.34290
DUK101	HOPEDALE	-60.26700	55.34040
DUK102	HOPEDALE	-60.26450	55.33970
DUK103	HOPEDALE	-60.26410	55.33890
DUK104	HOPEDALE	-60.26830	55.33830
DUK105	HOPEDALE	-60.27050	55.33750
DUK106	HOPEDALE	-60.27360	55.33690
DUK11	HOPEDALE	-59.92580	55.53860
DUK111	HOPEDALE	-59.96370	55.37920
DUK112	HOPEDALE	-59.81480	55.32900
DUK113	HOPEDALE	-59.81350	55.32880
DUK114	HOPEDALE	-59.81380	55.32820
DUK115	HOPEDALE	-59.81420	55.32700
DUK116	HOPEDALE	-59.81280	55.32970
DUK117	HOPEDALE	-59.81290	55.32860
DUK118	HOPEDALE	-59.81120	55.32890
DUK119	HOPEDALE	-59.81020	55.32840
DUK12	HOPEDALE	-59.91740	55.53720
DUK120	HOPEDALE	-59.80980	55.32700
DUK121	HOPEDALE	-59.81060	55.32570
DUK122	HOPEDALE	-59.80620	55.32530
DUK123	HOPEDALE	-59.80770	55.32470
DUK124	HOPEDALE	-59.80520	55.32380
DUK125	HOPEDALE	-59.80140	55.32420
DUK126	HOPEDALE	-59.94980	55.25910
DUK127	HOPEDALE	-59.94620	55.26000
DUK128	HOPEDALE	-59.94000	55.26270
DUK129	HOPEDALE	-60.07700	55.29180
DUK13	HOPEDALE	-59.86900	55.53780
DUK13.5	HOPEDALE	-59.87360	55.53570

DUK130	HOPEDALE	-60.12710	55.26180
DUK131	HOPEDALE	-60.13180	55.26460
DUK132	HOPEDALE	-60.12950	55.26370
DUK134	HOPEDALE	-60.31940	55.22180
DUK135	HOPEDALE	-60.05920	55.41450
DUK136	HOPEDALE	-60.08840	55.47250
DUK14	HOPEDALE	-59.92760	55.47960
DUK15	HOPEDALE	-59.92130	55.46750
DUK16	HOPEDALE	-59.93280	55.45450
DUK17	HOPEDALE	-59.93070	55.45740
DUK18	HOPEDALE	-60.10410	55.51600
DUK19	HOPEDALE	-60.09850	55.52400
DUK20	HOPEDALE	-60.10410	55.52910
DUK21	HOPEDALE	-60.09180	55.51580
DUK22	HOPEDALE	-60.07890	55.51130
DUK23	HOPEDALE	-60.08020	55.50190
DUK24	HOPEDALE	-60.07470	55.49740
DUK25	HOPEDALE	-60.07310	55.49410
DUK26	HOPEDALE	-60.06600	55.49300
DUK27	HOPEDALE	-60.05690	55.46270
DUK28	HOPEDALE	-60.04790	55.45450
DUK28.5	HOPEDALE	-60.04900	55.45490
DUK29	HOPEDALE	-60.06090	55.45600
DUK30	HOPEDALE	-60.05650	55.45130
DUK31	HOPEDALE	-60.08040	55.46800
DUK32	HOPEDALE	-60.13270	55.46430
DUK33	HOPEDALE	-60.04910	55.45100
DUK33.5	HOPEDALE	-60.04760	55.45140
DUK34	HOPEDALE	-60.05040	55.45230
DUK35	HOPEDALE	-60.02640	55.45020
DUK36	HOPEDALE	-59.96430	55.38520
DUK37	HOPEDALE	-59.96020	55.38600
DUK38	HOPEDALE	-59.96910	55.37940
DUK39	HOPEDALE	-59.95670	55.38250
DUK40	HOPEDALE	-59.95740	55.38360
DUK40.5	HOPEDALE	-59.95740	55.38360
DUK41	HOPEDALE	-59.95440	55.38640
DUK42	HOPEDALE	-59.95150	55.38950
DUK43	HOPEDALE	-59.93990	55.38710
DUK44	HOPEDALE	-59.94300	55.38510
DUK45	HOPEDALE	-59.84220	55.43470
DUK45.5	HOPEDALE	-59.84220	55.43460
DUK46	HOPEDALE	-59.88150	55.42390
DUK47	HOPEDALE	-59.88680	55.42220
DUK48	HOPEDALE	-59.88850	55.41790

DUK49	HOPEDALE	-59.88570	55.41780
DUK50	HOPEDALE	-59.89520	55.41780
DUK51	HOPEDALE	-60.10000	55.32250
DUK52	HOPEDALE	-60.09660	55.31970
DUK53	HOPEDALE	-60.04220	55.33490
DUK54	HOPEDALE	-60.04050	55.33600
DUK55	HOPEDALE	-60.03960	55.33400
DUK56	HOPEDALE	-60.11780	55.26800
DUK56.5	HOPEDALE	-60.11960	55.26770
DUK57	HOPEDALE	-60.11500	55.26310
DUK58	HOPEDALE	-60.13770	55.28400
DUK59	HOPEDALE	-60.13920	55.29190
DUK60	HOPEDALE	-60.13960	55.29520
DUK60.5	HOPEDALE	-60.14070	55.29420
DUK61	HOPEDALE	-60.14960	55.28980
DUK62	HOPEDALE	-60.21030	55.26260
DUK63	HOPEDALE	-60.29330	55.30490
DUK64	HOPEDALE	-60.07470	55.37190
DUK65	HOPEDALE	-59.98350	55.46210
DUK66	HOPEDALE	-60.09140	55.37830
DUK67	HOPEDALE	-60.45840	55.15860
DUK68	HOPEDALE	-60.38280	55.18370
DUK69	HOPEDALE	-60.07460	55.37520
DUK70	HOPEDALE	-60.05880	55.38220
DUK71	HOPEDALE	-60.05510	55.38170
DUK72	HOPEDALE	-59.91410	55.53070
DUK79	HOPEDALE	-60.08640	55.37630
DUK80	HOPEDALE	-60.88310	55.37570
DUK81	HOPEDALE	-60.08410	55.37370
DUK82	HOPEDALE	-60.07560	55.37450
DUK83	HOPEDALE	-59.93600	55.45890
DUK84	HOPEDALE	-59.93530	55.45790
DUK85	HOPEDALE	-59.92880	55.45560
DUK86	HOPEDALE	-59.92700	55.45770
DUK87	HOPEDALE	-59.92710	55.45580
DUK88	HOPEDALE	-59.93050	55.45950
DUK89	HOPEDALE	-59.92150	55.46170
DUK90	HOPEDALE	-59.76690	55.45390
DUK91	HOPEDALE	-59.76310	55.45410
DUK92	HOPEDALE	-59.76530	55.45640
DUK93	HOPEDALE	-59.76110	55.45810
DUK94	HOPEDALE	-59.76270	55.45890
DUK95	HOPEDALE	-59.76080	55.45950
DUK98	HOPEDALE	-59.79260	55.42150
DUK99	HOPEDALE	-59.79530	55.41860

MAK01	MAKKOVIK	-59.31990	55.31020
MAK02	MAKKOVIK	-59.35190	55.28500
MAK03	MAKKOVIK	-59.33290	55.25410
MAK04	MAKKOVIK	-59.33290	55.25410
MAK05	MAKKOVIK	-59.09440	55.16660
MAK06	MAKKOVIK	-59.09550	55.16250
MAK07	MAKKOVIK	-59.08830	55.16400
MAK08	MAKKOVIK	-59.06570	55.17360
MAK09	MAKKOVIK	-59.12990	55.21110
MAK10	MAKKOVIK	-59.12380	55.23600
MAK11	MAKKOVIK	-58.83300	55.01180
MAK12	MAKKOVIK	-58.82970	55.06980
MAK13	MAKKOVIK	-58.83240	55.07200
MAK14	MAKKOVIK	-58.93220	55.10900
MAK15	MAKKOVIK	-58.93350	55.10610
MAK16	MAKKOVIK	-58.94470	55.10890
MAK17	MAKKOVIK	-59.44540	55.19750
MAK18	MAKKOVIK	-59.44540	55.20210
MAK19	MAKKOVIK	-59.50060	55.23120
MAK20	MAKKOVIK	-59.61220	55.24030
MAK21	MAKKOVIK	-59.24230	55.25730
MAK22	MAKKOVIK	-59.25860	55.26130
MAK23	MAKKOVIK	-59.34400	55.24410
MAK24	MAKKOVIK	-59.35430	55.24360
MAK25	MAKKOVIK	-59.36630	55.24240
MAK26	MAKKOVIK	-59.36200	55.23900
MAK27	MAKKOVIK	-59.35600	55.24460
MAK28	MAKKOVIK	-58.81770	55.05170
MAK29	MAKKOVIK	-58.81950	55.05440
MAK30	MAKKOVIK	-58.84320	55.02070
MAK31	MAKKOVIK	-58.83290	55.01170
MAK32	MAKKOVIK	-58.72840	54.98610
MAK33	MAKKOVIK	-58.72760	54.98430
MAK34	MAKKOVIK	-58.72630	54.98620
MAK35	MAKKOVIK	-58.66140	54.98160
MAK36	MAKKOVIK	-58.66080	54.91780
MAK37	MAKKOVIK	-58.66370	54.91640
MAK38	MAKKOVIK	-59.44540	55.19750
MAK39	MAKKOVIK	-59.39000	55.29890
MAK40	MAKKOVIK	-59.39020	55.30340
MAK41	MAKKOVIK	-59.49100	55.22820
MAK42	MAKKOVIK	-59.50050	55.23120
MAK43	MAKKOVIK	-59.61220	55.24030
NDK01	NAIN	-61.34470	56.67630
NDK02	NAIN	-61.28210	56.77370

NDK04	NAIN	-61.26110	56.80540
NDK05	NAIN	-61.20810	56.82350
NDK06	NAIN	-61.20510	56.83300
NDK07	NAIN	-61.15610	56.88930
NDK08	NAIN	-61.28580	56.83630
NDK09	NAIN	-61.25520	56.73510
NDK10	NAIN	-61.19570	56.71020
NDK100	NAIN	-61.19390	56.34810
NDK101	NAIN	-61.18860	56.34920
NDK102	NAIN	-61.18780	56.34970
NDK103	NAIN	-61.18830	56.35100
NDK104	NAIN	-61.18660	56.35080
NDK105	NAIN	-61.18600	56.35090
NDK106	NAIN	-61.18420	56.35270
NDK11	NAIN	-61.13910	56.56250
NDK12	NAIN	-60.98490	56.55560
NDK13	NAIN	-61.05820	56.52930
NDK14	NAIN	-61.09940	56.48570
NDK15	NAIN	-61.08850	56.48810
NDK16	NAIN	-61.07710	56.48580
NDK17	NAIN	-61.07410	56.48320
NDK18	NAIN	-60.99390	56.45720
NDK18.5	NAIN	-60.99440	56.45620
NDK19	NAIN	-60.98360	56.46170
NDK20	NAIN	-60.98590	56.46480
NDK21	NAIN	-60.98520	56.46630
NDK22	NAIN	-60.98070	56.46580
NDK23	NAIN	-60.98270	56.46750
NDK24	NAIN	-61.16700	56.30770
NDK24.5	NAIN	-61.16700	56.30780
NDK25	NAIN	-61.18480	56.31150
NDK26	NAIN	-61.18640	56.29730
NDK27	NAIN	-61.17740	56.30650
NDK28	NAIN	-61.14980	56.31220
NDK29	NAIN	-61.05710	56.36680
NDK30	NAIN	-61.10180	56.37590
NDK31	NAIN	-61.18760	56.66180
NDK32	NAIN	-61.18280	56.67520
NDK33	NAIN	-61.17570	56.68810
NDK34	NAIN	-61.18810	56.68950
NDK35	NAIN	-61.18940	56.69330
NDK36	NAIN	-61.18940	56.69110
NDK36.5	NAIN	-61.19290	56.68790
NDK37	NAIN	-61.15110	56.70520
NDK38	NAIN	-61.12960	56.72970

NDK39	NAIN	-61.10890	56.72440
NDK40	NAIN	-61.18420	56.74920
NDK41	NAIN	-61.29140	56.77170
NDK42	NAIN	-61.77240	56.47010
NDK43	NAIN	-61.88330	56.41470
NDK44	NAIN	-61.03780	56.40740
NDK44.5	NAIN	-61.03870	56.40820
NDK45	NAIN	-61.43380	56.53720
NDK46	NAIN	-61.36860	56.47350
NDK47	NAIN	-61.43340	56.81790
NDK48	NAIN	-61.44150	56.81280
NDK49	NAIN	-61.45280	56.81400
NDK50	NAIN	-61.47130	56.80890
NDK51	NAIN	-61.47850	56.81390
NDK52	NAIN	-61.60620	56.40530
NDK53	NAIN	-61.61250	56.39950
NDK54	NAIN	-61.21450	56.33920
NDK55	NAIN	-61.20510	56.88390
NDK56	NAIN	-61.20560	56.83340
NDK57	NAIN	-61.19580	56.83440
NDK58	NAIN	-61.19350	56.83350
NDK59	NAIN	-61.19360	56.83300
NDK60	NAIN	-61.19590	56.83310
NDK61	NAIN	-61.20170	56.82860
NDK62	NAIN	-61.19290	56.83550
NDK63	NAIN	-61.21570	56.84310
NDK64	NAIN	-61.14500	56.83090
NDK65	NAIN	-61.19020	56.82970
NDK66	NAIN	-61.19000	56.82910
NDK67	NAIN	-61.19060	56.82880
NDK69	NAIN	-61.11310	56.73110
NDK70	NAIN	-61.10700	56.73110
NDK71	NAIN	-61.10520	56.73070
NDK72	NAIN	-61.11000	56.72700
NDK73	NAIN	-61.11420	56.72810
NDK74	NAIN	-61.11140	56.72550
NDK75	NAIN	-61.18720	56.69230
NDK76	NAIN	-61.19270	56.68870
NDK77	NAIN	-61.18350	56.30940
NDK78	NAIN	-61.18690	56.31220
NDK80	NAIN	-61.86840	56.45500
NDK81	NAIN	-61.68370	56.45250
NDK82	NAIN	-61.68680	56.45070
NDK83	NAIN	-61.69090	56.45110
NDK84	NAIN	-61.69100	56.45180

NDK85	NAIN	-61.69320	56.45260
NDK86	NAIN	-60.97540	56.46100
NDK87	NAIN	-60.98580	56.46010
NDK88	NAIN	-60.98400	56.45910
NDK89	NAIN	-61.13180	56.36010
NDK90	NAIN	-61.12710	56.35980
NDK91	NAIN	-61.12380	56.35880
NDK92	NAIN	-61.12460	56.36060
NDK93	NAIN	-61.12200	56.36190
NDK94	NAIN	-61.12200	56.36320
NDK95	NAIN	-61.11450	56.36340
NDK96	NAIN	-61.19570	56.34990
NDK97	NAIN	-61.19150	56.35270
NDK98	NAIN	-61.18550	56.35310
NDK99	NAIN	-61.18810	56.34840
OKA01	NAIN	-61.56160	57.22840
NWR01	NORTH WEST RIVER	-60.09890	53.64290
NWR02	NORTH WEST RIVER	-60.07190	53.66320
NWR03	NORTH WEST RIVER	-60.07280	53.66950
NWR04	NORTH WEST RIVER	-60.04060	53.66650
NWR05	NORTH WEST RIVER	-59.80310	53.84150
NWR06	NORTH WEST RIVER	-59.80270	53.79730
NWR07	NORTH WEST RIVER	-59.98960	53.71600
NWR08	NORTH WEST RIVER	-60.04340	53.65880
NWR09	NORTH WEST RIVER	-60.03290	53.66210
NWR10	NORTH WEST RIVER	-60.05130	53.66100
NWR11	NORTH WEST RIVER	-60.04130	53.65150
NWR12	NORTH WEST RIVER	-60.00920	53.66230
NWR13	NORTH WEST RIVER	-60.07180	53.55980
RIG01	RIGOLET	-58.99070	53.85600
RIG02	RIGOLET	-58.87150	53.93160
RIG03	RIGOLET	-58.86990	53.93310
RIG04	RIGOLET	-58.92290	54.01230
RIG05	RIGOLET	-58.70970	53.99420
RIG06	RIGOLET	-57.66950	54.47130
RIG07	RIGOLET	-57.66640	54.47120
RIG08	RIGOLET	-57.37590	54.55150
RIG09	RIGOLET	-57.38220	54.54830
RIG10	RIGOLET	-57.25300	54.53590
RIG11	RIGOLET	-57.22700	54.50310
RIG12	RIGOLET	-57.25030	54.47430
RIG13	RIGOLET	-57.22490	54.53230
RIG14	RIGOLET	-57.79810	54.37630
RIG15	RIGOLET	-57.67420	54.22280
RIG16	RIGOLET	-57.52940	54.21970

RIG17	RIGOLET	-57.52840	54.21930
RIG18	RIGOLET	-57.51060	54.22160
RIG19	RIGOLET	-57.50980	54.22700
RIG20	RIGOLET	-57.48630	54.22490
RIG21	RIGOLET	-57.41150	54.18940
RIG22	RIGOLET	-57.41410	54.18980
RIG23	RIGOLET	-57.40730	54.18250
RIG24	RIGOLET	-57.37950	54.21760
RIG25	RIGOLET	-57.40540	54.21950
RIG26	RIGOLET	-57.73450	54.21380
RIG27	RIGOLET	-58.19490	54.26340
RIG28	RIGOLET	-58.19460	54.26620
RIG29	RIGOLET	-57.93130	54.34670
RIG30	RIGOLET	-57.90370	54.37600
RIG31	RIGOLET	-57.86090	54.29770
RIG32	RIGOLET	-57.87060	54.29180
RIG33	RIGOLET	-57.82430	54.25770
RIG34	RIGOLET	-57.78410	54.22200
RIG35	RIGOLET	-57.80080	54.22610
RIG36	RIGOLET	-57.82840	54.22750
RIG37	RIGOLET	-57.84040	54.21430
RIG38	RIGOLET	-58.29240	54.21550
RIG39	RIGOLET	-58.29750	54.21550
RIG40	RIGOLET	-57.83490	54.21550
RIG41	RIGOLET	-58.07300	54.26440
RIG42	RIGOLET	-58.09210	54.25510
RIG43	RIGOLET	-57.80660	54.37580
RIG44	RIGOLET	-57.55180	54.20310
RIG45	RIGOLET	-58.93770	53.99500
RIG46	RIGOLET	-58.59140	54.00120
RIG47	RIGOLET	-58.53410	54.01940
RIG48	RIGOLET	-58.19490	54.26170
RIG49	RIGOLET	-58.93410	53.98870
RIG50	RIGOLET	-58.93300	53.98780
RIG51	RIGOLET	-58.90240	53.99590
RIG52	RIGOLET	-58.90200	53.99850
RIG53	RIGOLET	-58.90030	53.99830
RIG54	RIGOLET	-58.88830	53.99880
RIG55	RIGOLET	-58.89390	53.99590
RIG56	RIGOLET	-58.87290	53.99000
RIG57	RIGOLET	-58.87290	53.98990
RIG58	RIGOLET	-58.88940	53.98820
RIG59	RIGOLET	-58.89510	53.99770
RIG60	RIGOLET	-58.88190	53.99310
RIG61	RIGOLET	-57.88530	54.22210

RIG62	RIGOLET	-57.83530	54.21590
RIG63	RIGOLET	-57.68170	54.21090
RIG64	RIGOLET	-57.68080	54.20960
RIG65	RIGOLET	-57.68080	54.21310
RIG66	RIGOLET	-57.68230	54.21480
RIG67	RIGOLET	-57.67670	54.21460
RIG68	RIGOLET	-57.22350	54.53680
RIG69	RIGOLET	-57.84030	54.21440
RIG70	RIGOLET	-57.38150	54.55100
RIG71	RIGOLET	-57.36810	54.54930
RIG72	RIGOLET	-57.22330	54.53670
RIG73	RIGOLET	-57.22160	54.52920
RIG74	RIGOLET	-57.22600	54.53190
RIG75	RIGOLET	-57.22650	54.53300
RIG76	RIGOLET	-57.22500	54.53490
STP01	ST. PETER'S BAY	-55.68790	52.09900
STP02	ST. PETER'S BAY	-55.69250	52.09540
STP03	ST. PETER'S BAY	-55.69450	52.06550
STP04	ST. PETER'S BAY	-55.72560	52.04820
STP05	ST. PETER'S BAY	-55.73150	52.04580
STP06	ST. PETER'S BAY	-55.72050	52.03990
STP07	ST. PETER'S BAY	-55.72140	52.06560
STP08	ST. PETER'S BAY	-55.71710	52.06650
STP09	ST. PETER'S BAY	-55.71250	52.06980
STP10	ST. PETER'S BAY	-55.71150	52.07230
STP11	ST. PETER'S BAY	-55.73820	52.07480
STP12	ST. PETER'S BAY	-55.73600	52.07200
STP14	ST. PETER'S BAY	-55.74420	52.07840
STP15	ST. PETER'S BAY	-55.72460	52.07570

APPENDIX B. Nest counts of eiders by island and year. Note that in some cases only islands that were completely surveyed were used in analysis. Refer to appendix D, for information on search status by island and year.

ID	1998	1999	2000	2001	2002	2003	Total
DUK01	3	10	2		1	3	19
DUK02	1						1
DUK03	2	2			4		8
DUK04	6	3	1	4			14
DUK05	14	4	5	3	10	10	46
DUK06	38	39	28	25	52	86	268
DUK07	30	33	38		5		106
DUK08		2					2
DUK09	2						2
DUK10		9	4		14		27
DUK100						3	3
DUK101						2	2
DUK102						23	23
DUK104						2	2
DUK105						2	2
DUK11	4	1	1		2		8
DUK111						32	32
DUK119						57	57
DUK12		11	2		11		24
DUK120						17	17
DUK127						5	5
DUK13	4						4
DUK132						1	1
DUK134						40	40
DUK16	1			1	1		3
DUK17	4		1	1	6		12
DUK27			1				1
DUK28	17	13		15	8		53
DUK29	1	2	3				6
DUK31	2						2
DUK33					3		3
DUK33.5	1						1
DUK35	2	3		2	9		16
DUK36			1		1	6	8
DUK37	3	5	11	1	5	10	35
DUK38	2	4	2	1	14		23
DUK39	1					14	15
DUK40	2	1	1		1		5
DUK41	2	2	9	1	9	21	44
DUK43	15	13		5	24		57

DUK44	4				6		10
DUK45	1						1
DUK45.5	1						1
DUK47	3	5	4	7	9		28
DUK48					1		1
DUK50	3						3
DUK51	2						2
DUK52		2					2
DUK53	1						1
DUK55		1			11		12
DUK56	1	2	1		3	6	13
DUK56.5	3	2	1		1		7
DUK57	1	2	5		1		9
DUK58			2		3		5
DUK60	2	4	1	1	2		10
DUK61		5	3	2	4		14
DUK62	10	8	11	3	14		46
DUK63		8	6	28	10	28	80
DUK64		1	35	5	13	3	57
DUK65			12		7		19
DUK66			14	2		3	19
DUK67			30		10		40
DUK68			6	6	4		16
DUK69				20	1	2	23
DUK70				9			9
DUK72					79		79
DUK86						1	1
MAK18		3					3
MAK21		2					2
MAK25		1					1
MAK26		4					4
MAK28		1					1
MAK29		1					1
MAK30		2					2
MAK31		8					8
MAK36		1					1
MAK37		28					28
MAK38		7					7
MAK39		1					1
MAK42		4					4
MAK43		45					45
NDK02	2						2
NDK04	6	57	4	28	49		144
NDK05	73	42	48	7	45	1	216
NDK06	9	17	10	12	4	7	59

NDK08	2						2
NDK09	8	5	28	6	32	16	95
NDK10	19	23	11	22	21	29	125
NDK11	3	11					14
NDK12	19						19
NDK13	2						2
NDK14	7	5	4		10	40	66
NDK15	1						1
NDK16	13	10	15	20	38	44	140
NDK17	6	12	30	24	42	40	154
NDK18	1				34		35
NDK19	12	15	40	53	74		194
NDK20	2	3	5		13		23
NDK21	2	5		40	53		100
NDK22	51		42	46	46		185
NDK24					50	74	124
NDK25	7				11		18
NDK26	19	18	28	19	10		94
NDK27	11				24		35
NDK28	36	66	87	62			251
NDK29	53	53	46	63	70		285
NDK30	11	6	8	8	2		35
NDK31		3					3
NDK32		8	1		10	17	36
NDK33	13	24	14		37		88
NDK35	2	1	1				4
NDK37	15				79		94
NDK38	6	23	35	74	110	37	285
NDK39	41	100	84		272	192	689
NDK40	63	40	1	16	45	17	182
NDK42		81					81
NDK44			78	76		78	232
NDK45			2				2
NDK46			4				4
NDK47			1				1
NDK50			1				1
NDK54				7			7
OKA01	16						16
RIG02			1		2		3
RIG03					1		1
RIG04			2	7	10	13	32
RIG05			11	2	7		20
RIG06			193			261	454
RIG07			212			165	377
RIG08			59			64	123

RIG09		27		25	52
RIG10			209	188	397
RIG12		2			2
RIG13		648	646	654	1948
RIG14		88	53	73	84	298
RIG15		290			290
RIG16				1	1
RIG17		36		1	37
RIG18		274	66	32	372
RIG19		21		70	91
RIG21			129	94	223
RIG22			5	9	14
RIG23		35	38	63	136
RIG25		197	231	243	671
RIG26		43		26	29	98
RIG28		18			18
RIG29				283	283
RIG31		107	98	103	109	417
RIG32			290	181	264	735
RIG34		102	175	151	170	598
RIG35		3	12	22	37
RIG36		6	76	88	93	263
RIG37		10			10
RIG41				5	19	24
RIG42				7	13	20
RIG43				25	25
RIG44				29	29
RIG47				5	5
RIG61					2	2
RIG63					8	8
RIG65					6	6
RIG66					32	32
RIG68					3	3
STP03	91			109	200
STP04	117			124	241
STP05	13			2	15
STP06				86	86
STP07	3				3
STP08	33			30	63
STP09				7	7
STP11	29		51	22	102
STP12	164		215	111	490
STP14	56		58	30	144
STP15				1	1
STP16				178	178

STP17					16		16
GRAND TOTAL	720	1439	3254	3086	3787	3171	15457

APPENDIX C. Nest counts of large gulls (Great Black Backed and Herring Gulls) by island and year. Note that in some cases only islands that were completely surveyed were used in analysis. Refer to appendix D, for information on search status by island and year.

ID	1998	1999	2000	2001	2002	2003	Total
DUK01	1	2			1	1	5
DUK02	1	3					4
DUK03	1	1					2
DUK03.5	1						1
DUK04		2		2			4
DUK05	2	2					4
DUK06	2	3	2		2	3	12
DUK07	1	1	3				5
DUK09	1						1
DUK10	1	1	2				4
DUK100						1	1
DUK101						1	1
DUK102						1	1
DUK11	1	1	3				5
DUK111						1	1
DUK119						1	1
DUK12		1			1		2
DUK120						1	1
DUK127						10	10
DUK13	1						1
DUK132						1	1
DUK134						1	1
DUK16	3	1	2				6
DUK17			2				2
DUK18		1					1
DUK21	5						5
DUK22	4	1	4				9
DUK23		3	1		1		5
DUK25	1						1
DUK26		2					2
DUK27	2		1				3
DUK28	4	3	5				12
DUK29		2	5	1			8
DUK30	1	1	1				3
DUK31	1						1
DUK33	1						1
DUK34	2						2
DUK35	1	1	2	1	1		6

DUK36	1		3	1		1	6
DUK37		1	2			2	5
DUK38	1	2					3
DUK39	1					1	2
DUK40	2	1	7			1	11
DUK41	1	1	1		1	1	5
DUK43	9	3		3	2		17
DUK44	3						3
DUK47	1	1	2	1	1		6
DUK51	1		2				3
DUK52	1	1	1				3
DUK53	1	1	1				3
DUK55			1		1		2
DUK56		2					2
DUK56.5		1	1		1		3
DUK57		1	2				3
DUK58	1	1	1				3
DUK60	1	1					2
DUK60.5	1	1					2
DUK61	3	7	8	1	1		20
DUK62	3		2		1		6
DUK63		1	1				2
DUK64		1	1	1		1	4
DUK65			1				1
DUK66			1	1		1	3
DUK67			10				10
DUK68			2	1			3
DUK69				1			1
DUK70				1			1
MAK06		3					3
MAK17		1					1
MAK18		1					1
MAK21		6					6
MAK22		37					37
MAK25		3					3
MAK26		3					3
MAK27		1					1
MAK31		2					2
MAK34		1					1
MAK37		3					3
MAK42		2					2
MAK43		2					2
NDK02	2						2
NDK03	1						1
NDK04		2	2	1			5

NDK05	3	1	1				5
NDK06	1	1	1			1	4
NDK07	1						1
NDK08	1						1
NDK09		1	2	1		1	5
NDK10	1	1	3	1		2	8
NDK11	2	2					4
NDK12	2						2
NDK14	1						1
NDK15			1				1
NDK16	1	1	2			1	5
NDK17	3	2	1		1		7
NDK18					1		1
NDK19		1	1	1	1		4
NDK20		1					1
NDK21	1			1			2
NDK22	1						1
NDK24						2	2
NDK25	1						1
NDK26		1	1	1	1		4
NDK27	1						1
NDK28		1	1				2
NDK29	1			1	3		5
NDK30	1	1	1	1			4
NDK31		1					1
NDK32			1		1	1	3
NDK33		1	1		1		3
NDK34	2						2
NDK37	1						1
NDK38	2		1	1			4
NDK39	1	1	2		1		5
NDK40	1		1				2
NDK42		2					2
NDK44				1		1	2
NDK45		1	1				2
NDK46			4				4
NDK47			4				4
NDK48			1				1
NDK49			2				2
NDK50			20				20
NWR09				1			1
NWR12					33		33
OKA01	1						1
RIG01			23				23
RIG04			200	5			205

RIG04B			28				28
RIG05			3	4	2		9
RIG06			1			1	2
RIG07			7			2	9
RIG08						1	1
RIG09			7			3	10
RIG10				11		13	24
RIG12			10				10
RIG13				6		28	34
RIG14				1	2	1	4
RIG15			10				10
RIG17			8				8
RIG18			4	3	6		13
RIG19			4		21		25
RIG21				2	2		4
RIG22				1	5		6
RIG23			3	2	4		9
RIG25			4	5	8		17
RIG26			9	15	7	4	35
RIG28			2				2
RIG29					28		28
RIG31			3	2	3	2	10
RIG32				24	15	29	68
RIG34				7	5	6	18
RIG35					1		1
RIG36				3	2	2	7
RIG40				2			2
RIG43					12		12
RIG44					12		12
RIG47					1		1
RIG63						1	1
STP01		12					12
STP02		9		5			14
STP03		140					140
STP04		101					101
STP05		10					10
STP07		11					11
STP08		41					41
STP11		6		8			14
STP12		228		120			348
STP14		36		19			55
GRAND TOTAL	102	740	464	271	193	132	1902

APPENDIX D. Search effort by island and year. The codes are as follows. C = Complete search; B = Boat searched; N = Not searched; P = Partial search. Note that in many cases only islands that were completely searched were used in analyses in this thesis, please refer to methods in each chapter for more detail.

ID	1998	1999	2000	2001	2002	2003
DUK01	C	C	C	N	C	C
DUK02	C	C	N	N	C	N
DUK03	C	C	C	N	C	N
DUK03.5	C	N	N	N	N	N
DUK04	C	C	C	C	C	C
DUK05	C	C	C	C	C	C
DUK06	C	C	C	C	C	C
DUK07	C	C	C	N	C	N
DUK08	C	C	N	N	N	N
DUK09	C	N	N	N	N	N
DUK10	C	C	C	N	C	N
DUK100	N	N	N	N	N	C
DUK101	N	N	N	N	N	C
DUK102	N	N	N	N	N	C
DUK103	N	N	N	N	N	C
DUK104	N	N	N	N	N	C
DUK105	N	N	N	N	N	C
DUK106	N	N	N	N	N	C
DUK11	C	C	C	N	C	N
DUK111	N	N	N	N	N	C
DUK112	N	N	N	N	N	C
DUK113	N	N	N	N	N	C
DUK114	N	N	N	N	N	C
DUK115	N	N	N	N	N	B
DUK116	N	N	N	N	N	B
DUK117	N	N	N	N	N	B
DUK118	N	N	N	N	N	B
DUK119	N	N	N	N	N	C
DUK12	C	C	C	N	C	N
DUK120	N	N	N	N	N	C
DUK121	N	N	N	N	N	B
DUK122	N	N	N	N	N	B
DUK123	N	N	N	N	N	B
DUK124	N	N	N	N	N	B
DUK125	N	N	N	N	N	B
DUK126	N	N	N	N	N	B
DUK127	N	N	N	N	N	C
DUK128	N	N	N	N	N	B
DUK129	N	N	N	N	N	B

DUK13	C	N	N	N	N	N
DUK13.5	C	N	N	N	N	N
DUK130	N	N	N	N	N	B
DUK131	N	N	N	N	N	C
DUK132	N	N	N	N	N	C
DUK134	N	N	N	N	N	C
DUK135	N	N	N	N	N	C
DUK136	N	N	N	N	N	C
DUK14	C	N	N	N	N	N
DUK15	C	N	N	N	N	N
DUK16	C	C	C	C	C	C
DUK17	C	C	C	C	C	C
DUK18	C	C	N	N	N	N
DUK19	C	C	N	N	N	N
DUK20	C	N	N	N	N	N
DUK21	C	B	N	N	N	N
DUK22	C	C	C	C	C	N
DUK23	C	C	C	N	C	N
DUK24	C	N	N	N	C	N
DUK25	C	N	N	N	N	N
DUK26	C	C	N	N	N	N
DUK27	C	C	C	C	C	N
DUK28	C	C	P	C	N	N
DUK28.5	C	N	N	N	C	N
DUK29	C	C	C	C	N	N
DUK30	C	C	C	B	N	N
DUK31	C	N	N	N	C	N
DUK32	C	N	N	N	N	N
DUK33	C	N	N	N	C	N
DUK33.5	C	N	N	N	C	N
DUK34	C	N	N	N	N	N
DUK35	C	C	C	C	C	N
DUK36	C	N	C	C	C	C
DUK37	C	C	C	C	C	C
DUK38	C	C	C	N	C	N
DUK39	C	N	N	N	C	C
DUK40	C	C	C	C	C	C
DUK40.5	B	N	N	N	N	N
DUK41	C	C	C	C	C	C
DUK42	C	N	C	N	N	C
DUK43	C	C	N	C	C	N
DUK44	C	N	N	N	C	N
DUK45	C	B	N	N	N	N
DUK45.5	C	N	N	N	N	N
DUK46	C	N	N	N	C	N

DUK47	C	C	C	C	C	N
DUK48	C	N	C	N	C	N
DUK49	C	N	C	N	N	N
DUK50	C	C	C	N	N	N
DUK51	C	C	C	C	C	N
DUK52	C	C	C	N	C	N
DUK53	C	C	C	N	C	N
DUK54	C	C	C	N	C	N
DUK55	C	C	C	N	C	N
DUK56	C	C	C	B	C	C
DUK56.5	C	C	C	C	C	B
DUK57	C	C	C	N	C	C
DUK58	C	C	C	N	C	N
DUK59	C	C	C	N	C	N
DUK60	C	C	C	C	C	N
DUK60.5	C	C	N	N	C	N
DUK61	C	C	C	P	C	N
DUK62	C	C	C	C	C	N
DUK63	N	C	C	C	C	C
DUK64	N	C	C	C	C	C
DUK65	N	N	C	C	C	N
DUK66	N	N	C	C	N	C
DUK67	N	N	C	N	C	N
DUK68	N	N	P	C	C	N
DUK69	N	N	N	C	C	C
DUK70	N	N	N	C	N	N
DUK71	N	N	N	C	N	N
DUK72	N	N	N	N	C	N
DUK79	N	N	N	N	N	B
DUK80	N	N	N	N	N	B
DUK81	N	N	N	N	N	B
DUK82	N	N	N	N	N	B
DUK83	N	N	N	N	N	B
DUK84	N	N	N	N	N	B
DUK85	N	N	N	N	N	B
DUK86	N	N	N	N	N	C
DUK87	N	N	N	N	N	C
DUK88	N	N	N	N	N	C
DUK89	N	N	N	N	N	B
DUK90	N	N	N	N	N	B
DUK91	N	N	N	N	N	B
DUK92	N	N	N	N	N	B
DUK93	N	N	N	N	N	B
DUK94	N	N	N	N	N	B
DUK95	N	N	N	N	N	B

DUK98	N	N	N	N	N	B
DUK99	N	N	N	N	N	B
NDK01	C	C	C	N	B	N
NDK02	C	N	N	N	C	N
NDK04	C	C	C	C	C	N
NDK05	C	C	C	C	C	C
NDK06	C	C	C	C	C	C
NDK07	C	N	N	N	N	N
NDK08	C	N	N	N	N	N
NDK09	C	C	C	C	C	C
NDK10	C	C	C	C	C	C
NDK100	N	N	N	N	N	B
NDK101	N	N	N	N	N	B
NDK102	N	N	N	N	N	B
NDK103	N	N	N	N	N	B
NDK104	N	N	N	N	N	B
NDK105	N	N	N	N	N	B
NDK106	N	N	N	N	N	B
NDK11	C	C	N	N	N	N
NDK12	C	N	N	N	N	N
NDK13	C	B	N	N	N	N
NDK14	C	C	C	N	C	C
NDK15	C	N	C	N	C	N
NDK16	C	C	C	C	C	C
NDK17	C	C	C	C	C	C
NDK18	C	N	N	N	C	N
NDK18.5	C	N	N	N	N	N
NDK19	C	C	C	C	C	N
NDK20	C	C	C	N	C	N
NDK21	C	C	N	C	C	N
NDK22	C	N	C	C	C	N
NDK23	C	C	N	N	C	N
NDK24	C	N	N	N	C	C
NDK25	C	N	N	N	C	B
NDK26	C	C	C	C	C	N
NDK27	C	N	N	N	C	B
NDK28	C	C	C	C	N	N
NDK29	C	C	C	C	C	N
NDK30	C	C	C	C	C	N
NDK31	C	C	N	N	N	N
NDK32	C	C	C	N	C	C
NDK33	C	C	C	N	C	N
NDK34	C	N	N	N	N	B
NDK35	C	C	C	N	N	B
NDK36	C	N	N	N	N	B

NDK36.5	C	N	N	N	N	B
NDK37	C	N	N	N	C	N
NDK38	C	C	C	C	C	P
NDK39	C	C	C	N	C	C
NDK40	C	C	C	C	C	C
NDK41	C	C	C	N	N	N
NDK42	N	C	N	N	N	N
NDK43	N	B	N	N	N	N
NDK44	N	P	C	C	N	C
NDK44.5	N	B	N	N	N	N
NDK45	N	C	C	N	N	N
NDK46	N	C	C	N	C	N
NDK47	N	C	C	N	N	N
NDK48	N	C	C	N	N	N
NDK49	N	B	C	N	N	N
NDK50	N	B	C	N	N	N
NDK51	N	B	C	N	N	N
NDK52	N	B	N	N	N	N
NDK53	N	B	N	N	N	N
NDK54	N	N	N	C	N	N
NDK55	N	N	N	N	N	B
NDK56	N	N	N	N	N	B
NDK57	N	N	N	N	N	B
NDK58	N	N	N	N	N	B
NDK59	N	N	N	N	N	B
NDK60	N	N	N	N	N	B
NDK61	N	N	N	N	N	B
NDK62	N	N	N	N	N	B
NDK63	N	N	N	N	N	B
NDK64	N	N	N	N	N	B
NDK65	N	N	N	N	N	N
NDK66	N	N	N	N	N	B
NDK67	N	N	N	N	N	B
NDK69	N	N	N	N	N	B
NDK70	N	N	N	N	N	B
NDK71	N	N	N	N	N	B
NDK72	N	N	N	N	N	B
NDK73	N	N	N	N	N	B
NDK74	N	N	N	N	N	B
NDK75	N	N	N	N	N	B
NDK76	N	N	N	N	N	B
NDK77	N	N	N	N	N	B
NDK78	N	N	N	N	N	B
NDK80	N	N	N	N	N	B
NDK81	N	N	N	N	N	B

NDK82	N	N	N	N	N	B
NDK83	N	N	N	N	N	B
NDK84	N	N	N	N	N	B
NDK85	N	N	N	N	N	B
NDK86	N	N	N	N	N	B
NDK87	N	N	N	N	N	B
NDK88	N	N	N	N	N	B
NDK89	N	N	N	N	N	B
NDK90	N	N	N	N	N	B
NDK91	N	N	N	N	N	B
NDK92	N	N	N	N	N	B
NDK93	N	N	N	N	N	B
NDK94	N	N	N	N	N	B
NDK95	N	N	N	N	N	B
NDK96	N	N	N	N	N	B
NDK97	N	N	N	N	N	B
NDK98	N	N	N	N	N	B
NDK99	N	N	N	N	N	C
RIG01	N	N	N	N	N	N
RIG02	N	N	C	N	C	N
RIG03	N	N	C	C	C	N
RIG04	N	N	C	C	C	C
RIG05	N	N	C	N	P	N
RIG06	N	N	C	N	N	C
RIG07	N	N	C	N	N	C
RIG08	N	N	C	N	N	C
RIG09	N	N	C	C	N	C
RIG10	N	N	C	N	N	C
RIG11	N	N	C	N	N	N
RIG12	N	N	B	C	N	N
RIG13	N	N	C	C	N	C
RIG14	N	N	C	N	C	C
RIG15	N	N	C	N	N	N
RIG16	N	N	P	N	C	N
RIG17	N	N	C	C	C	N
RIG18	N	N	C	N	C	N
RIG19	N	N	C	N	C	N
RIG20	N	N	C	C	N	N
RIG21	N	N	B	P	C	N
RIG22	N	N	B	P	C	N
RIG23	N	N	B	N	C	N
RIG24	N	N	P	C	N	N
RIG25	N	N	B	C	C	N
RIG26	N	N	C	N	C	C
RIG27	N	N	C	N	N	N

RIG28	N	N	B	N	N	N
RIG29	N	N	C	N	C	N
RIG30	N	N	C	C	B	N
RIG31	N	N	B	P	C	C
RIG32	N	N	C	B	C	C
RIG33	N	N	B	C	N	N
RIG34	N	N	B	C	C	C
RIG35	N	N	C	C	C	N
RIG36	N	N	C	N	C	C
RIG37	N	N	C	P	C	C
RIG38	N	N	C	P	P	N
RIG39	N	N	B	C	P	N
RIG40	N	N	B	N	N	C
RIG41	N	N	N	N	P	P
RIG42	N	N	N	N	P	P
RIG43	N	N	N	N	C	N
RIG44	N	N	N	N	C	N
RIG45	N	N	N	N	C	C
RIG46	N	N	N	N	B	N
RIG47	N	N	N	N	C	N
RIG48	N	N	N	N	P	N
RIG49	N	N	N	N	N	B
RIG50	N	N	N	N	N	B
RIG51	N	N	N	N	N	B
RIG52	N	N	N	N	N	B
RIG53	N	N	N	N	N	B
RIG54	N	N	N	N	N	B
RIG55	N	N	N	N	N	B
RIG56	N	N	N	N	N	B
RIG57	N	N	N	N	N	B
RIG58	N	N	N	N	N	B
RIG59	N	N	N	N	N	B
RIG60	N	N	N	N	N	B
RIG61	N	N	N	N	N	C
RIG62	N	N	N	N	N	C
RIG63	N	N	N	N	N	C
RIG64	N	N	N	N	N	C
RIG65	N	N	N	N	N	C
RIG66	N	N	N	N	N	C
RIG67	N	N	N	N	N	B
RIG68	N	N	N	N	N	C
RIG69	N	N	N	N	N	B
RIG70	N	N	N	N	N	B
RIG71	N	N	N	N	N	B
RIG72	N	N	N	N	N	C

RIG73	N	N	N	N	N	N
RIG74	N	N	N	N	N	B
RIG75	N	N	N	N	N	B
RIG76	N	N	N	N	N	B
STP01	N	C	N	C	C	N
STP02	N	C	N	N	C	N
STP03	N	C	N	N	C	N
STP04	N	C	N	N	C	N
STP05	N	C	N	N	C	N
STP06	N	B	N	N	C	N
STP07	N	C	N	N	N	N
STP08	N	C	N	N	C	N
STP09	N	B	N	N	C	N
STP10	N	B	N	C	N	N
STP11	N	C	N	C	C	N
STP12	N	C	N	C	C	N
STP14	N	C	N	C	C	N
STP15	N	N	N	N	C	N
STP16	N	N	N	N	C	N
STP17	N	N	N	N	C	N